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POPULATION ECOLOGY OF GAMMARUS LACUSTRIS SARS
IN BIG ISLAND LAKE

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

JUNE 1966

THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Population ecology of Gammarus lacustris Sars in Big Island Lake," submitted by Poimplasserì Sivaramakrishna Menon in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

The objective of the present investigation was to study some of the ecological aspects of the Gammarus lacustris population in Big Island Lake, Alberta, with reference to its habitat preference, relative abundance, life cycle, age, growth, size and sex ratio. The study extended over a period of two years, 1964 to 1966.

The distribution of gammarids during summer months showed that they preferred shallow shores with emergent and submerged aquatic vegetation. In the open lake, they showed marked preference for the bottom layer as compared with surface and middle layers. A 24 hour study (July 31-August 1, 1965) showed a diel variation in the horizontal distribution of the population.

The life cycle is annual. Pairing of the sexes (precopula) occurs in early spring preparatory to ovulation, copulation and fertilization. The ova are carried by the female in the ventral brood pouch. In Big Island Lake, most female have only a single brood, the size of which varies in direct relation to body length. Most females die after release of the first brood, while a few surviving females reproduce a second time. The early brood of May and June, in 1965, took four weeks for incubation, while the second brood in July of the same year, took only two weeks. The mean water temperatures for the two periods were 14.9°C. and 22.0°C. respectively.

Five stages in life cycle have been distinguished: (i) immature (newborn to 2-month old), (ii) juvenile (2 to 5 months old), (iii) pre-reproductive (5 to 10 months old), (iv) reproductive (10 to 13 months old), and (v) post-reproductive (13 months and over). The average span of life

is about 13 months. The approximate percentage duration of the three ecological ages are (a) developmental = 88.6%, (b) reproductive = 7.6% and (c) post-reproductive = 3.8%.

Sex ratios were equal in the juvenile and reproductive stages (summer) while males outnumbered females in the pre- and post-reproductive stages, (winter).

In relation to total abundance, low numbers were observed in the early spring of 1965, when the gammarid population showed a restricted age distribution being mainly composed of reproductive adults. With the rapid recruitment of the new generation, the population level rose to a peak in July, followed by an equally rapid decline due to early mortality of immatures. By the end of August the population was almost half of the peak level. Besides predation by aquatic birds, carnivorous insect larvae and nymphs, winter mortality also affected the population, mostly during March, when anoxic conditions prevailed in the lake.

A brief account of the epibionts and parasites is given. Finally, a few observations have been made on the ecological adaptations which have made this species a very successful member of the lake community.

ACKNOWLEDGEMENTS

I wish to acknowledge my deep gratitude to Dr. J. R. Nursall for suggesting this problem and for the guidance, advice and encouragement which have always been a source of inspiration to me during the course of my study. I wish to thank Dr. J. C. Holmes for the interest he showed in the study from the start. To Dr. H. F. Clifford and Dr. D. A. Boag, are my sincere thanks for their help and valuable suggestions from time to time. I am indebted to Dr. G. O. Mackie and Dr. D. M. Ross for the personal interest they always showed in my work.

Thanks are also due to Mr. Keith Winchell for his field assistance and Miss M. Harris for laboratory assistance in the summer of 1965. To Mr. J. Nuis, Mr. J. Kerekes, Mr. M. Denny and Mr. L. C. Graham are my thanks for their willing cooperation during my trips to the lake.

I am thankful to Mr. E. Bosniak for identifying plant materials. I am particularly grateful to Mr. S. K. Krishnaswamy who helped me in the preparation of figures and graphs. For the analysis of water samples, I wish to thank the Provincial Analyst, Alberta.

To my wife, Padma, I am grateful for all the help she rendered during the course of this work and for the statistical analysis of the data.

Financial support was provided by the University of Alberta, National Museum of Canada and N.R.C. operating grants of Dr. J. R. Nursall.

TABLE OF CONTENTS

	Page
I. INTRODUCTION	1
II. METHODS	4
III. THE LAKE ENVIRONMENT	9
Temperature	12
Oxygen	13
pH	13
IV. HABITAT PREFERENCE AND RELATIVE ABUNDANCE	15
May 1965	16
June 1965	17
July 1965	19
August 1965	20
September 1965	20
October 1965	21
Vertical distribution in open lake	23
Horizontal shift in open lake	24
V. LIFE CYCLE	29
Sexual dimorphism	29
Precopula	33
Fertilization	34
Fecundity	34
Fertility	37
Incubation period	39
VI. AGE, GROWTH AND SIZE	41

	Page
VII. POPULATION STRUCTURE	48
January 1965	48
February 1965	53
March 1965	55
April 1965	55
May 1965	56
June 1965	58
July 1965	60
August 1965	62
September 1965	63
October 1965	65
November 1965	66
December 1965	67
VIII. SEX RATIO	68
IX. MORTALITY	77
X. LONGEVITY	81
XI. EPIBIONTS AND PARASITES	84
XII. DISCUSSION	89
Population dynamics	92
SUMMARY	101
BIBLIOGRAPHY	105
APENDICES	110
Appendix I: Physical and chemical characteristics of the water samples	110
Appendix II: Details of the samples against sampling dates	112

Appendix III: Two-factor analysis of variance.

Months and Habitats 113

Appendix IV: Two-factor analysis of variance.

Months and layers in open lake 115

Appendix V: Single-factor analysis of variance to see

the differences in means between surface,

middle and bottom layers 116

LIST OF TABLES

	Page
Table 1. Estimated numbers of gammarids per 100 liters of sample from the different habitats. Mean values for the months of May to October, 1965	16
Table 2. Layers in the order of preference indicated by X	24
Table 3. Twenty-four hour distribution of gammarids in the open lake (gammarids/100 liters) July 31 - August 1, 1965	26
Table 4. Body length of female and seasonal fecundity...	35
Table 5. Mean body length of gammarids showing approx- imate age in days after birth, June-October, 1965	42
Table 6. Stages in the life cycle of <u>Gammarus lacustris</u> showing approximate number of moults and mean body length in mm.	43
Table 7. Percentage composition of <u>Gammarus</u> population January 1965 and 1966	48
Table 8. Percentage composition of <u>Gammarus</u> population February 1965 and 1966	53
Table 9. Percentage composition of <u>Gammarus</u> population March 1965 and 1966	55
Table 10. Percentage composition of <u>Gammarus</u> population May 1965	56
Table 11. Percentage composition of <u>Gammarus</u> population June 1965	58

List of tables cont'd.

	Page
Table 12. Percentage composition of <u>Gammarus</u> population	
July 1965	60
Table 13. Percentage composition of <u>Gammarus</u> population	
August 1965	62
Table 14. Percentage composition of <u>Gammarus</u> population	
September 1965	63
Table 15. Percentage composition of <u>Gammarus</u> population	
October 1965	65
Table 16. Percentage composition of <u>Gammarus</u> population	
November 1965	66
Table 17. Percentage composition of <u>Gammarus</u> population	
December 1965	67
Table 18. <u>Gammarus</u> population. Sex ratio (%)	
1964 - 1965 and 1966	70
Table 19. Relative duration of ecological ages in	
<u>Gammarus lacustris</u>	82

LIST OF FIGURES

	Page
Fig. 1. Outline map of Big Island Lake	10
Fig. 2. Monthly mean values of temp., pH, and dissolved oxygen	14
Fig. 3. Histogram showing relative abundance	18
Fig. 4. 24-hour vertical distribution in the open lake..	27
Fig. 5. <u>Gammarus lacustris</u> . Diagrams showing secondary sexual characters in adult male and female	30
Fig. 6. <u>Gammarus lacustris</u> . Diagram of 7th peraeonic segment in male showing genital papillae...	31
Fig. 7. <u>Gammarus lacustris</u> . Diagrams of oostegite in female.....	32
Fig. 8. Mean brood size and range	36
Fig. 9. Number of gravid females per hundred	38
Fig. 10. Mass growth-curve	44
Fig. 11. Percentage composition of <u>Gammarus</u> population samples. Jan., Feb., and March, 1965 and 1966	49
Fig. 12. Percentage composition of <u>Gammarus</u> population samples. May, June, and July, 1965	50
Fig. 13. Percentage composition of <u>Gammarus</u> population samples. July and August, 1965	51
Fig. 14. Percentage composition of <u>Gammarus</u> population samples. Sept., Oct., Nov., and Dec., 1965	52

List of figures cont'd

	Page
Fig. 15. Percentage duration of ecological ages	83
Fig. 16. Population growth curve	96

I. INTRODUCTION

Gammarus lacustris Sars is a freshwater crustacean belonging to the family Gammaridae under the order Amphipoda. Popularly they are known by various names such as "scuds", "side-swimmers", sea-weed lice, beach fleas and "shrimps" (a term more aptly used for some decapod Crustacea). Fritz Johansen (1920) in his account of the larger freshwater Crustacea of Canada and Alaska mentioned two species, Gammarus fasciatus and Gammarus limnaeus being found in Canada, of which G. limnaeus has the widest distribution. Subsequently, Shoemaker (1955) synonymized G. limnaeus with G. lacustris, and in 1958 Bousfield established two subspecies under G. lacustris, namely G. lacustris lacustris and G. lacustris limnaeus. Of these, G. lacustris lacustris has a wider distribution. It is found in the Northwest Territories and the provinces of British Columbia, Alberta, Saskatchewan, Manitoba, Ontario and Quebec in Canada, and the states of Idaho, Wyoming, California and New Mexico in the U. S. A. G. lacustris limnaeus is more restricted in its distribution to Ontario, Quebec and Newfoundland in Canada, and Minnesota in the U. S. A.*

The present investigation was undertaken to study the population ecology of G. lacustris lacustris, found in the Big Island Lake, Alberta, hereafter referred to as G. lacustris. Our knowledge of the taxonomy, general biology, and economic importance of the North American species of gammarids is largely based upon the work of Thomas Say (1818), Weckel (1907),

* G. lacustris is also reported from England and countries of Northwestern Europe and U. S. S. R.

Huntsman (1915), Johansen (1920), Hubricht and MacKin (1940), Shoemaker (1942), and Bousfield (1958). Cussans (1904) in her monograph on Gammarus pulex provided a detailed study of the morphology and anatomy of this freshwater amphipod, and a later work by Clemens (1950) on Gammarus fasciatus in the Lake Erie habitat contributed invaluable information on the ecology, behavior, breeding habits and life cycle of the species.

There are few studies on the population ecology of macroinvertebrates, particularly freshwater amphipods. The work of Hynes (1955) on the reproductive cycle of British freshwater gammarids deserves special mention, and has provided impetus for the present study. Clemens (1950) devoted a small section of his account on G. fasciatus to discuss the population dynamics of this species. Clifford (1965) in his studies of an intermittent stream of south-central Indiana, described the reproductive cycles of two univoltine species, Lirceus fontinalis and Crangonyx forbesi. Cooper (1965) gave a descriptive account of the population dynamics in Hyaella azteca, a species which is often found in association with G. lacustris.

The present study on the population ecology of Gammarus lacustris, was felt necessary, considering the importance of this organism, not only as a rich source of food for fishes and aquatic birds, but also as a well established intermediate host for the transmission of acanthocephalan and cestode parasites of vertebrates. Besides, there are many advantages in the choice of Gammarus lacustris as a subject for ecological study, which may be listed.

1. They are found in great abundance and are available throughout the year. They are able to withstand the severe conditions of the winter months when the lakes are under ice-cover, and maintain a population level sufficient to

give rise to the observed high level in summer.

2. They form a continuous population, somewhat indifferent to the substratum as long as there is enough shelter or cover. They are catholic in their feeding habits and can thrive on any kind of organic matter providing detritus on which they can feed.

3. They have a strictly annual life cycle, the majority of the females reproducing only once (univoltine), and most of the immatures being recruited within a short period of one month.

4. From the time the juveniles are 2 months old, the sexes are distinguishable and the sex-ratios can be recorded.

5. During the breeding season, the female bears the brood in the brood pouch and accurate counts of the brood can be made.

As against the advantages mentioned, the one serious disadvantage is the great numbers in which they occur during the summer months. This is a challenging problem for sampling purposes.

II. METHODS

A general survey of Big Island Lake with reference to the preferred habitats of G. lacustris was carried out during the summer of 1964. It was found that gammarids were not randomly distributed but showed considerable variation in density of population between the different habitats in the lake. With a view to obtaining as representative a sample as possible, collection techniques had to be devised, suitable for each habitat under the prevailing conditions. It was felt necessary to take samples regularly from the habitats specified below.

- a) The open lake with scant submerged vegetation.
- b) The very shallow shores lined by the emergent vegetation of cattails, brome grass and burreed.
- c) The shallow muddy shores.
- d) The sandy shores.
- e) Those regions of the lake where Potamogeton vegetation appeared abundantly during the months of June through October.

Systematic sampling of these areas was carried out in the summer of 1965, May through October.

The open lake was the most variable among the habitats mentioned as far as density distribution of Gammarus population was concerned, and accordingly larger sampling fractions had to be taken. Collections were made from three different levels (i) the surface layer within 0.5 m. depth (ii) the middle layer approximately between 0.5 and 1 m. below the surface and (iii) the bottom layer 1.5 to 2 m. below the surface, which was close to the bottom.

Four polyethylene bottles were tied in a series at 4 meter intervals to

a long rope and were set afloat using lead blocks as anchors. These could be shifted with ease, and the same set of floats was used at different sites in the open lake. The length of the anchor rope was adjusted every time so that the floats were right at the surface, and the connecting rope between the floats held them in position. Even during windy weather this was found to be quite stable. The boat was driven by a 3 h.p. outboard motor at very low speed in a straight line close to the floats and the collection was made between two adjacent floats, dragging the net horizontally for a distance of 4 meters. The three collections from the surface layer, middle layer and bottom layer were taken in succession, between different pairs of floats. Care was taken to avoid undue disturbance to the collection site.

A circular #1 mm. mesh nylon dip net, 1000 sq. cm. in area and 50 cm. long was used. Such a net, could withstand not only the thrust, but also it could catch the smallest gammarids including the new born, which measured only 2 to 2.5 mm. in body length. While drawing the net between floats, a certain force was necessary to hold the net in the vertical position, particularly while taking the sample from the bottom layer. The collected sample from each layer was immediately transferred to numbered bottles and fixed in 5% formalin. Normally, on the same day of collection, three widely separated sites in the open lake were selected for such sampling and on different days different sites were chosen to avoid selection bias.

The collection from the area of Potamogeton, during the months of June through October 1965 was made also using the same technique, with the difference that the net was drawn along a distance of only 1 meter, thus scanning 100 liters of water at a time, as compared with the 400 liter sample from the open lake. It was necessary to limit the sampling to a smaller

size, because of great and uniform abundance of gammarids in this area.

Collections from the cattail areas were restricted to the shallow shores not more than 35 cm. deep. A hollow drum of galvanized iron 15 cm. in diameter and 40 cm. high was kept in place over the area to prevent gammarids moving away. After stirring up the contents, 10 liters of the water was filtered through a smaller hand net of the same #1 mm. mesh nylon. The material thus collected was preserved in 5% formalin for subsequent sorting in the laboratory. Three such samples were collected from widely separated parts of the shoreline on each day of sampling.

The same method was employed for the shallow sandy shores and mud shores. The sandy shore formed only a very small fraction of the entire shoreline, and collection in this area had to be abandoned when the water level rose due to the heavy rains during the last week of June 1965, and gammarids had spread over the flooded land. However, in estimating the total abundance for the month of July, the flooded area was also considered as a part of the sandy shore.

The shallow mud shores were sampled only during the months of May and June prior to the establishment of rooted vegetation along the shores.

Occasional samples of bottom mud were collected with an Ekman dredge. As the number of gammarids found in the bottom mud samples was negligibly few, no regular sampling was deemed necessary by this method. Apparently the bottom mud was favored as a habitat only during the winter months, when shelter in the form of aquatic vegetation was minimal.

In the laboratory, the collected samples were thoroughly washed, sifted and the specimens sorted out into adults, immatures and juveniles according

to the season, separate counts being maintained. The only other amphipod present in the samples, was Hyalella azteca which was easily distinguished. With some experience, even the newly born immatures of the two could be separated under the binocular microscope.

After having separated all the gammarids into adults, juveniles and immatures, they were preserved in fresh 5% formalin for future measurements.

For determining the sex-ratio, one lot of about 200 individuals from each well-mixed sample of adults and juveniles was taken at random, and the males and females were separated under the binocular microscope on the basis of the secondary sexual characters, namely calceoli and genital papillae in the males, and the presence of oostegites and absence of calceoli in the female. Sexes could not be distinguished in the immature stages until they became juveniles, about 2 months old.

From the sorted samples for each date of collection, 50 males and 50 females were selected at random, and kept in water for a period of 30 minutes, which was sufficient to make them flexible enough for handling. To measure the body length, from the tip of the head to the base of the telson, each specimen was straightened against a millimeter scale rigidly supported on a glass slide. Readings were taken to the nearest millimeter. Immatures and juveniles also were measured in the same manner.

During the breeding season, counts of brood carried by the females, were taken by gently teasing out the contents of the brood pouch into a watch glass.

Examination of specimens for the presence of acanthocephalan and cestode cysts was done by squeezing out the contents of the body on a slide. In most cases the cystacanths were visible through the integument but not the smaller cestode cysts for which the method outlined above was quite suitable.

Observations on living specimens were carried out in the laboratory for which aquaria were maintained at room temperature 17^o to 20^oC. In these aquaria, plants such as Vallisneria, and Ceratophyllum provided shelter. A thin layer of the lake mud was also provided in these aquaria. Gammarids thrived very well in these aquaria, and occasionally were provided with fish food.

Most of the collections in the lake were carried out between 9 AM and 12 Noon, a time during which gammarids were very active, and when less windy conditions prevailed. Measurements of temperature, oxygen content and pH were taken during each sampling trip. A simple centigrade thermometer was used for temperature readings. For pH determination, a portable Beckman pocket pH meter, Model 180, was used. Oxygen estimations were carried out in the field, using the method described by Miller (1914). Secchi disc readings also were taken.

For analysis of water samples, a commercial chemical kit (Model DR-EL Hach Chemical Company, Iowa) was employed.

III. THE LAKE ENVIRONMENT

Big Island Lake is a shallow eutrophic lake, located about 17 miles southeast of Edmonton, Alberta, covering an area of approximately 300 acres (121.4 hectares). Much of the lake is less than two meters deep, the maximum depth recorded being 2.5 m at a few places. The overall extent of the shoreline is considerably increased by the presence of an island in the middle of the lake, with an area of about 12 acres (4.8 hectares). The entire shoreline is dominated by the emergent vegetation chiefly composed of cattail, Typha latifolia; reed grass, Phragmites communis; brome grass, Bromus erectus and burreed, Sparganium sp. In certain areas along the shoreline, Sagittaria cuneata was also present, appearing rather late in summer. Between these plants the water was found to be less than a half meter deep.

During May and June (1964 and 1965), the shallow littoral zone, next to the cattail area did not show any rooted vegetation. This area in most parts of the lake had a muddy bottom, very rich in autochthonous organic detritus. Sandy shore was found only in two places along the shoreline, which had a sandy bottom (Fig. 1).

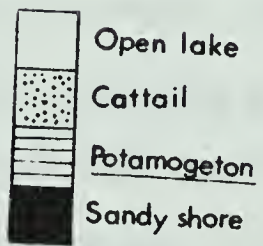
By the middle of June, rooted vegetation began to establish itself all along the shallow shores down to a depth of about 1.5 m. The two species which dominated the littoral habitat were Potamogeton richardsoni and Potamogeton pectinatus. In some places the zone of rooted submerged vegetation extended about 15 to 20 m. into the lake. Similar vegetation was also present around the island. Among other aquatic plants, can be mentioned Lemna trisulca (found mostly in clumps towards the bottom), Lemna minor (floating), Ceratophyllum demersum and Myriophyllum exalbescens (submerged).

Figure 1. Outline map of Big Island Lake, showing areas covered by open lake, cattail, Potamogeton and sandy shore (July 1965).

FIG. 1

Big Island Lake.

Scale : 1 cm. = 0.157 km.



The animal life of the lake in general was found to be rich in numbers. Gammarus lacustris was evidently the most abundant macroinvertebrate. The only other amphipod, found in moderate abundance, was Hyallela azteca, which shared the cattail and Potamogeton habitats with gammarids. A variety of leeches, Helobdella stagnalis, Erpobdella punctata, Theromyzon rude and Glossiphonia complanata were present in addition to Lumbriculus sp. and many Tubificidae (Oligochaeta). Among the molluscs, a few gastropods such as Lymnaea stagnalis and Physa sp. were found in plenty. Hydrachnids and many insect larvae and nymphs of Odonata, Trichoptera, Coleoptera, Hemiptera and Diptera were present. Among these, dytiscids (Coleoptera) and Enallagma sp. (Odonata) were most abundant. Among the dipterans, chironomids and Chaoborus sp. were predominant.

Fishes were conspicuously absent, probably due to the shallow nature of the lake and extreme winter stagnation. Muskrats and beavers were occasionally observed swimming in the lake.

During the spring and summer months several aquatic birds were transitory residents of the lake. Most common were the grebes, Podiceps grisegena (red-necked grebe), Podiceps auritus (horned grebe), and Podiceps caspicus (eared grebe). Among other birds which were less common can be mentioned the following: Larus pipixcan (Franklin's gull), Oxyura jamaicensis (ruddy duck), Melanitta deglandi (white-winged scoter), Aythya affinis (lesser scaup), and Anas platyrhynchos (mallard).

Most of these birds fed avidly on gammarids.

The zooplankton during the summer months contained teeming myriads of Daphnia sp. along with Cyclops sp. and Diaptomus sp. June and July were

the months of greatest plankton abundance. Ostracods such as Candona sp. and Cypridopsis sp. were also present. Among the many ciliates, forms such as Vorticella sp. and colonial Epistylis sp., Zoothamnium sp. and Carchesium sp. were found to live as epibionts on gammarids. Several rotifers were present. Brachionus sp., Trichocera sp. and Rotaria neptunia were in great abundance.

The phytoplankton was equally rich. Blooms of Anabaena flos-aquae, Anabaena circinalis, Aphanizomenon flos-aquae, Microcystis aeruginosa, and Microcystis flos-aquae, gave a grass-green color to the lake water during the months of June and July. Also present in great numbers, were Pediastrum borianum, Pediastrum duplex, Scenedesmus sp. among the green algae, and Melosira sp., Cyclotella sp., and Navicula sp. among the diatoms.

During the winter months the lake remained completely ice covered. In 1964-1965, the ice cover lasted from the first week of November until the first week of May. Considerable depletion of plant and animal life occurred towards the peak of winter stagnation in the month of March, when there was no demonstrable oxygen in the lake and H_2S was present.

The physical and chemical characteristics of the lake water are given in Appendix I.

Temperature

The temperature curve for the six-month period, May through October, 1965, is shown in Fig. 2. From a mean temperature of $12^{\circ}C$ observed in May, there was a steady rise towards July, when the mean temperature recorded was $22^{\circ}C$. The maximum temperature recorded was $25.9^{\circ}C$ on August 3, 1965. The downward trend in temperature began in August, and by October the mean

temperature for the month was 6.5°C . During the winter months of 1964-1965, the water temperature varied only slightly between 2° and 1°C . This was the period when the ice cover was about 2 feet thick with 1 foot of snow above.

Oxygen

The dissolved oxygen concentration during the period May to October 1965 varied (Fig. 2). A mean of 6.1 cc/liter (90% saturation) for the month of May was observed. In July, it was 4.3 cc/liter (77% saturation). Thereafter there was a steady rise in oxygen as is expected with the falling temperatures. By October the oxygen level reached 7.7 cc/liter (100% saturation).

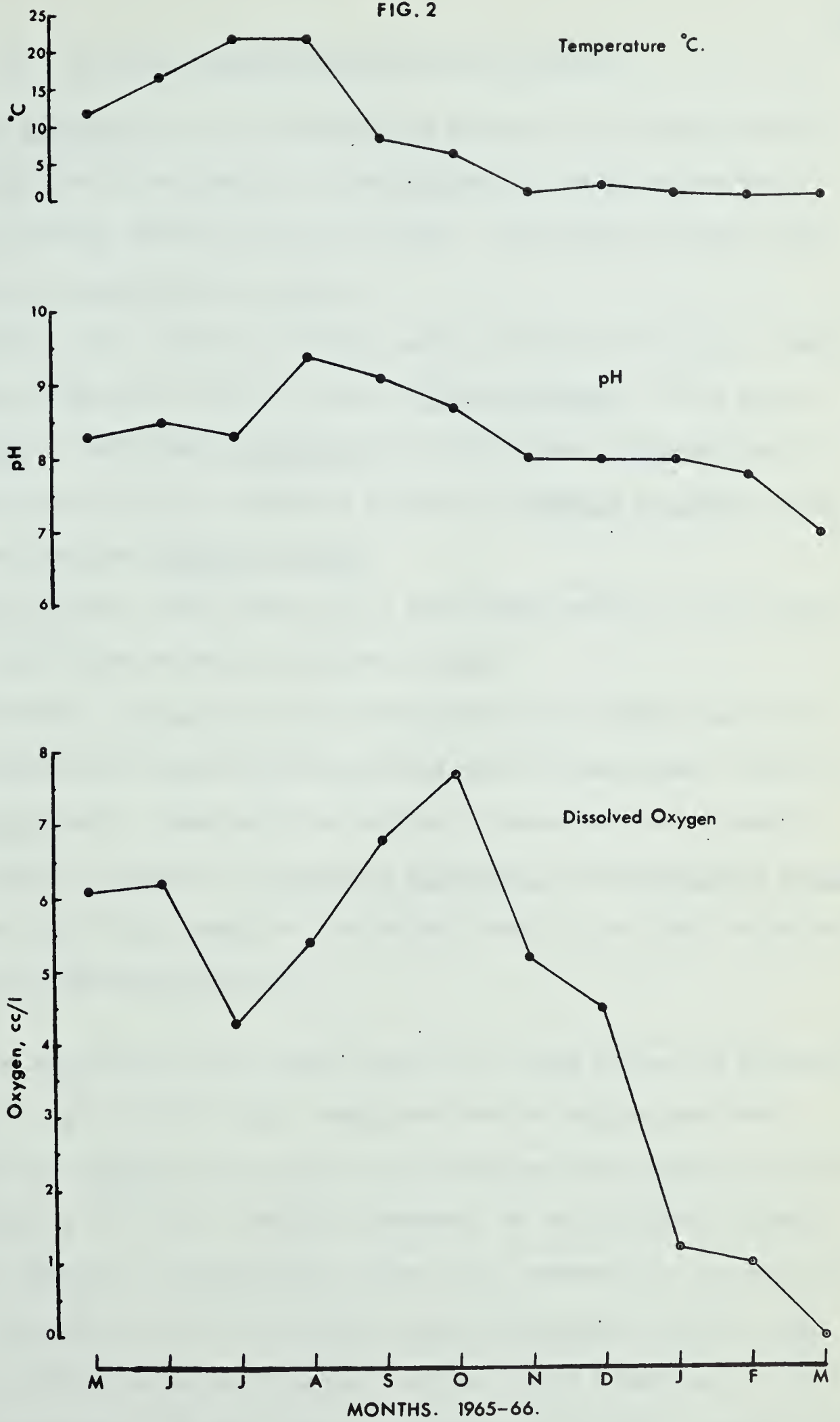
During the winter months, when the lake was fully ice-covered, the dissolved oxygen content showed a gradual decline from 5.2 cc/liter (58% saturation) in November to 1 cc/liter (11% saturation) in January and February. During the month of March, no oxygen was found to be present. At this time about 0.5 ppm of H_2S was present.

pH

The mean pH varied from 7.0 during winter months to a maximum of 9.4 recorded for the month of August. The pH values for the months of May, June and July were 8.3, 8.5, and 8.3 respectively (Fig. 2).

Figure 2. Monthly mean values of temperature ($^{\circ}\text{C}.$), pH, and dissolved oxygen (cc/l) recorded in Big Island Lake, for the period May 1965 to March 1966.

FIG. 2



IV. HABITAT PREFERENCE AND RELATIVE ABUNDANCE

Gammarus lacustris can be collected from any part of the lake, but the observed variations in the density of the population clearly showed their preference to certain habitats within the lake. The various habitats could be conveniently categorized as follows:

1. The cattail area - this area extends along the entire shoreline, composed of the emergent vegetation chiefly cattail (Typha latifolia), brome grass (Bromus erectus), reed grass (Phragmites sp.) and burreed (Sparganium sp.). This area was found to be the preferred habitat of Gammarus lacustris, along with the other amphipod, Hyalella azteca.
2. The sandy shores - this formed only a very small fraction of the entire shoreline. The bottom was mainly composed of sand.
3. The mud shores - alongside to the cattail areas, the shallow mud shore was mainly composed of autochthonous materials which formed organic detritus.
4. Potamogeton area - these were the regions of submerged rooted aquatic vegetation chiefly composed of Potamogeton richardsoni and Potamogeton pectinatus.
5. The open lake - this comprised the central areas of the lake, characterized by scanty submerged vegetation.

It may be mentioned at the outset that at all times during the six-month period, May through October (1965), when quantitative sampling was done, it was found that Gammarus was abundant in the shallow shore among the cattails. In the description to follow, a monthly statement of the population density (expressed as numbers of gammarids/100 liters) with reference to the habitats is given on the basis of the mean density figures calculated from the total samples for the month collected from each habitat (Table 1 and Fig. 3). For purposes of comparison, the open lake is considered as one unit, though collections were made from three different levels as already mentioned. The

collections for the first and second halves of June are treated separately in the table, as this shows more clearly the rapid shift in numbers with the recruitment of the new generation. Further details of the samples are given in Appendix II.

Table 1 - Estimated numbers of gammarids per 100 liters of sample from the different habitats. Mean values for the months May - October, 1965

Habitat	Month						
	May	June (1-13)	June (14-30)	July	August	Sept.	Oct.
open lake	22.20	11.01	12.41	35.88	29.31	13.50	18.57
cattail	598.00	225.50	1776.00	1507.75	1748.25	1233.33	966.00
sandy shore	28.00	136.25	1388.00	3207.50	-	-	-
mud shore	1060	230.00	-	-	-	-	-
<u>Potamogeton</u>	-	-	-	661.85	273.46	229.30	418.15
Total	1708.20	602.76	3176.41	5412.98	2015.02	1476.13	1402.72
Grand mean	427.05	150.69	1058.80	1353.24	683.67	492.04	467.57

May - 1965

This was a period just after the thawing of ice and when there was no submerged aquatic vegetation. Greater numbers of gammarids were observed along the mud shores with an average abundance of 1060 gammarids/100 liters. This was to be expected as it was a continuation of the condition observed during winter months when the overwintering population survived mostly on the organic detritus found in the mud. With the thawing of ice and the partial establish-

ment of the cattail vegetation, gammarids began to invade this area, which was frozen solid until recently, and showed a density of 598 gammarids/100 liters. The open lake and sandy shores had comparatively few individuals, 22 gammarids/100 liters and 28 gammarids/100 liters respectively. All samples for the month of May taken together showed a grand mean of 427 gammarids/100 liters which represented the population density for the whole lake in the month of May.

The entire May population was composed of reproductive adults which formed the parent population.

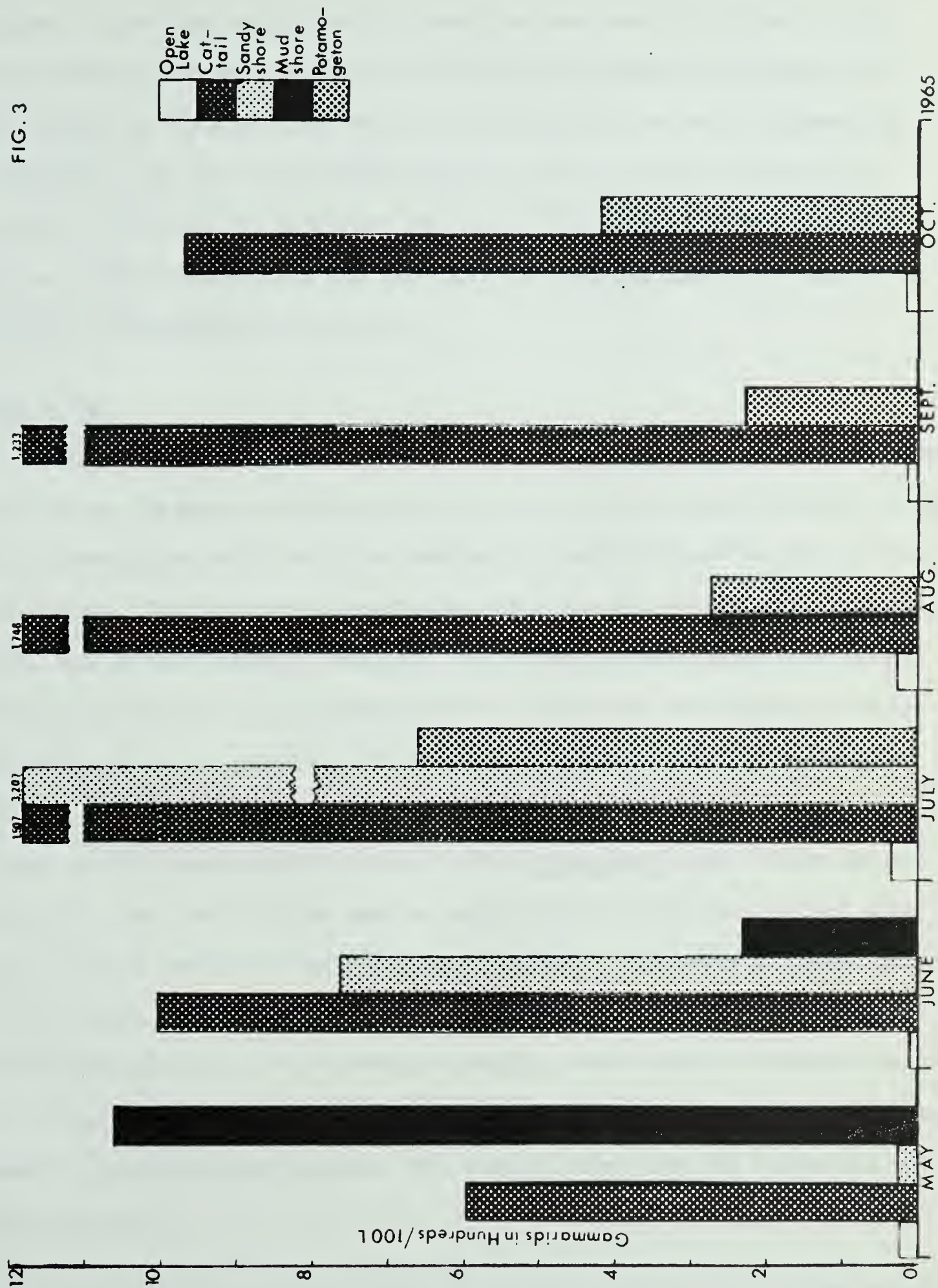
June - 1965

Changes in the distribution pattern became evident in the month of June. This was also a period when the recruitment of the new generation began. The shoreline vegetation was well established and there was gradual decline in the number of individuals inhabiting the mud shores, which showed a mean density of 230 gammarids/100 liters during the first half of June. For the same period, the mean density of gammarid population for the sandy shore was 136 gammarids/100 liters and 225 gammarids/100 liters for the cattail area and only 11 gammarids/100 liters in the open lake. The overall reduction in the mean population density during the first half of June, prior to the recruitment of the new generation, was mainly due to the mortality experienced by the adult population at a time of rapid change, and partly due to predation by aquatic birds which had recently arrived.

During the second half of June, because of the recruitment of immatures into the population, a rapid increase in numbers was noticed. The two habitats which showed the greatest density of population were the cattail area with 1776 gammarids/100 liters and the sandy shores with 1388 gammarids/100

Figure 3. Histogram showing relative abundance of gammarids
(No. X 100 gammarids/100 liters) in the habitats
sampled May to October 1965. (Based on Table 1.)

FIG. 3



2117-8

[REDACTED]

[REDACTED]

[REDACTED]

[REDACTED]

[REDACTED]

[REDACTED]

[REDACTED]

[REDACTED]

liters. Since the newly recruited immatures were mostly confined to the shores where there was shelter, the effect of increase in population was not evident in the open lake where the mean density was only 12 gammarids/100 liters. The mud shore samples failed to show the high numbers seen earlier. Excluding the mud shore habitat, which was no longer preferred, the mean population density for the whole lake during the second half of June was 1058 gammarids/100 liters.

July - 1965

July was the month of maximum abundance with respect to the whole gammarid population. As much of the parent population died off after the first brood was released, the newly recruited immatures formed the major section of the population. The Potamogeton vegetation, which was well-established by this time, was another preferred habitat. The estimated mean population density for the whole lake was 1353 gammarids/100 liters with the relative density distributions of 35 gammarids/100 liters in the open lake, 1507 gammarids/100 liters in the cattail area, 3207 gammarids/100 liters along the sandy shores and 661 gammarids/100 liters in the Potamogeton area. Heavy showers during the last week of June made an appreciable rise in the level of water and a certain section of the population drifted to the newly submerged land near the lake. Samples collected from such areas were included under the sandy shore habitat, as the previous sampling sites were no longer accessible due to the high level of water. This probably accounted for the high numbers observed along the sandy shores. Mud samples taken from the bottom did not show gammarids,

Thus, with the overall increase in shelter in the form of rooted aquatic vegetation, combined with the rapid recruitment of the new generation, the

peak density figure was observed for July, in spite of the slight dispersion brought about by the floods.

August - 1965

The samples taken during the month of August, were confined to the three habitats, open lake, cattail and Potamogeton, not taking into account the special situation created by the floods. Moreover, the flood waters had receded considerably, and the original sandy shores could not be sampled as they were still too deep. Of the three habitats sampled, only the cattail area showed a slight increase in the density from 1507 gammarids/100 liters to 1748 gammarids/100 liters in August. This was partly due to the retreat of gammarids with the receding water, and partly due to the release of the second brood during the second half of July. The Potamogeton area showed a mean population density of 273 gammarids/100 liters and the open lake area showed 29 gammarids/100 liters.

The overall population density for the month of August was 683 gammarids/100 liters almost half of the level observed in July. Early mortality of the immatures and the mortality experienced by the parent population after the reproduction must have contributed to this decline. In addition, some individuals must also have died, being stranded on the land, as the water receded.

Only 1% of the total August population was adults, the remaining 99% were immatures and juveniles.

September - 1965

The density distribution of the samples in September was somewhat similar to those in August, except that there was a slight reduction in numbers, notice-

able in all the three habitats. The mean density for the month was 492 gammarids/100 liters. The relative distributions were 13 gammarids/100 liters in the open lake, 1233 gammarids/100 liters in the cattail area, and 229 gammarids/100 liters in the Potamogeton area.

The surviving post-reproductive adults of the parent population constituted 2% of the total, as compared with 1% in August, because of the slight decrease in numbers of juveniles due to mortality, (discussed elsewhere, p.78).

October - 1965

Samples were taken only twice during this month, just prior to the winter freeze-up. Gammarids still showed their preference for the cattail and Potamogeton habitats. As compared to the density figure of 18 gammarids/100 liters for the open lake, cattail area showed 966 gammarids/100 liters and Potamogeton area showed 418 gammarids/100 liters. The mean density, observed for the whole lake was 467 gammarids/100 liters, which should be considered as the density level prior to the onset of winter.

As the density figures expressed for specified habitats were based on many replicate samples for the same period, they should be a fair estimate of the relative abundance of gammarids. It was evident that greater numbers of gammarids were always found in association with the emergent and submerged aquatic vegetation, which showed the importance of shelter as a governing factor in their spatial distribution. When such shelter was not available, as for example during the winter months, and at the beginning of spring in the month of May, they were mostly found close to the mud, whereas in the summer months of June, July and August, they were hardly to be found near the mud. The versatility of gammarids to exploit all available habitats according to particular seasons of the year must be a

natural outcome of their liberal feeding habits as well. Restriction of the reproductive period to that part of the year when there is an overall increase of shelter within the lake must have contributed much to the successful maintenance of population levels.

On the basis of the observations, it could be stated that the abundance of gammarids in a lake environment depended not so much on the total extent of the open waters of the lake, but on the presence of a shoreline with emergent vegetation and the occurrence of ample rooted vegetation in the littoral zone.

To determine whether there was any statistical validity in the above statement, a two factor analysis of variance was done on the population means obtained from the different habitats (following Simpson, Roe and Lewontin, 1960, page 280). Details of analysis are presented in Appendix III.

The F for months was not significant. However the difference between the habitats was found to be highly significant at the .01 level. The interaction between month and habitat was also not significant.

Thus, it was clearly evident that gammarids showed preference to particular habitats, regardless of seasonal variations in population structure.

From the time the Potamogeton vegetation was well established in the lake, it was a preferred habitat for gammarids. This habitat was compared with the cattail area using a two-tailed t-test. The results were significant at the .01 level ($P. t_0 \geq 11.41 = < .01$). The mean population in the cattail area was significantly higher than in the Potamogeton area.

Vertical distribution in open lake

In comparison with the other habitats, the density figures for the open lake appeared low and negligible. But, considering the fact that the total space available in the open lake was far greater than in any other habitat, samples were collected from the three layers, surface, middle and bottom, throughout the six-month period. Generally speaking the open lake served as a buffer zone relieving the pressures of population density in the preferred habitats. This was also the area where gammarids cruised about swimming when they were active. Irrespective of the time of day, gammarids always showed a preference for the bottom layer of water which was about 1.5 to 2.5 meters below the surface. For example in the month of July, the mean densities for the three layers were found to be 19.6 gammarids/100 liters in the surface layer, 37.8 gammarids/100 liters in the middle layer and 54.8 gammarids/100 liters in the bottom layer.

Another two-factor analysis of variance was carried out to see whether any significant difference was present in the vertical distribution of the gammarids in the open lake (details are given in Appendix IV).

All the F ratios were found to be significant, the months and layers at the .01 level, and the interactions at the .05 level. A marked preference for a definite layer was also evident. It is also interesting to note that while the mean differences between months were not significant when the lake was considered as a whole, they were highly significant when only the open lake was taken into account. This may be explained on the basis of the increase in population brought about by the rapid recruitment during the months of June and July, and consequent greater dispersion of the population into open lake. This would probably account for the interaction between layers and months also.

As the collections in the open lake were made from three different layers, surface, middle and bottom, it was felt necessary to find out whether there was any significant difference between the layers. For this, only the July samples were analyzed, as this was the period of maximum abundance.

A single-factor analysis of variance was done. Details are presented in Appendix V.

The F ratio was significant at the .01 level. Following a significant overall F, the Newman-Keuls' test (Steel and Torrie, 1960, p. 110) was administered to determine which of the three layers was preferred most by gammarids (Table 2).

Table 2. Layers in the order of preference indicated by X

Layer	Surface	Middle	Bottom
Surface	-	X	X
Middle	-	-	X
Bottom	-	-	-

It was found that the mean population in the bottom layer was significantly higher than the other two layers. Similarly, the middle layer was found to have a significantly higher population mean than the surface layer.

Horizontal shift in the open lake

With a view to clarifying some of the observations made regarding density distributions at the three different levels in the open lake, it was felt

necessary to carry out quantitative sampling over a period of 24 hours, at intervals of 2 hours, to see if any diurnal shifts occurred in the population. Floats were set up at a chosen station and samples were collected from the three different levels, at specified intervals of 2 hours starting at 6 PM and ending at 6 PM the next day. The data presented are based on the collections made on July 31 and August 1, 1965. On these two days the lake was quite calm and there was practically no disturbance due to wind. Also being a period of maximum density of population, this was considered to be a good time for such a study.

It is seen from Table 3 and Figure 4 that the maximum abundance in the open lake occurred at 10 AM when there were 421 gammarids/100 liters and the minimum at 12 Midnight with only 23 gammarids/100 liters. The vertical distribution at 10 AM showed 143 gammarids/100 liters in the surface layer, 234 gammarids/100 liters in the middle layer and 888 gammarids/100 liters in the bottom layer. As compared to this, at 12 Midnight, the bottom layer showed only 18 gammarids/100 liters, whereas the surface layer and middle layer showed 20.5 gammarids/100 liters and 31.5 gammarids/100 liters respectively. Apparently though there was an overall reduction in the population density at midnight, the fact that relatively more gammarids were found in the surface and middle layers at this time, showed that during the dark hours of the night they leave the bottom layer and come up more towards the surface. Between these two extremes, a certain regularity is observed in the changing patterns of density distributions as is clear from the graph. The two peaks, one at 10 PM and the other at 10 AM clearly showed that these were two equally spaced periods of activity, of which the more active period was between 8 AM and 12 Noon, when the higher peak was

Table 3. Twenty-four hour distribution of gammarids
in the open lake (gammarids/100 liters)
(July 31 - Aug. 1, 1965)

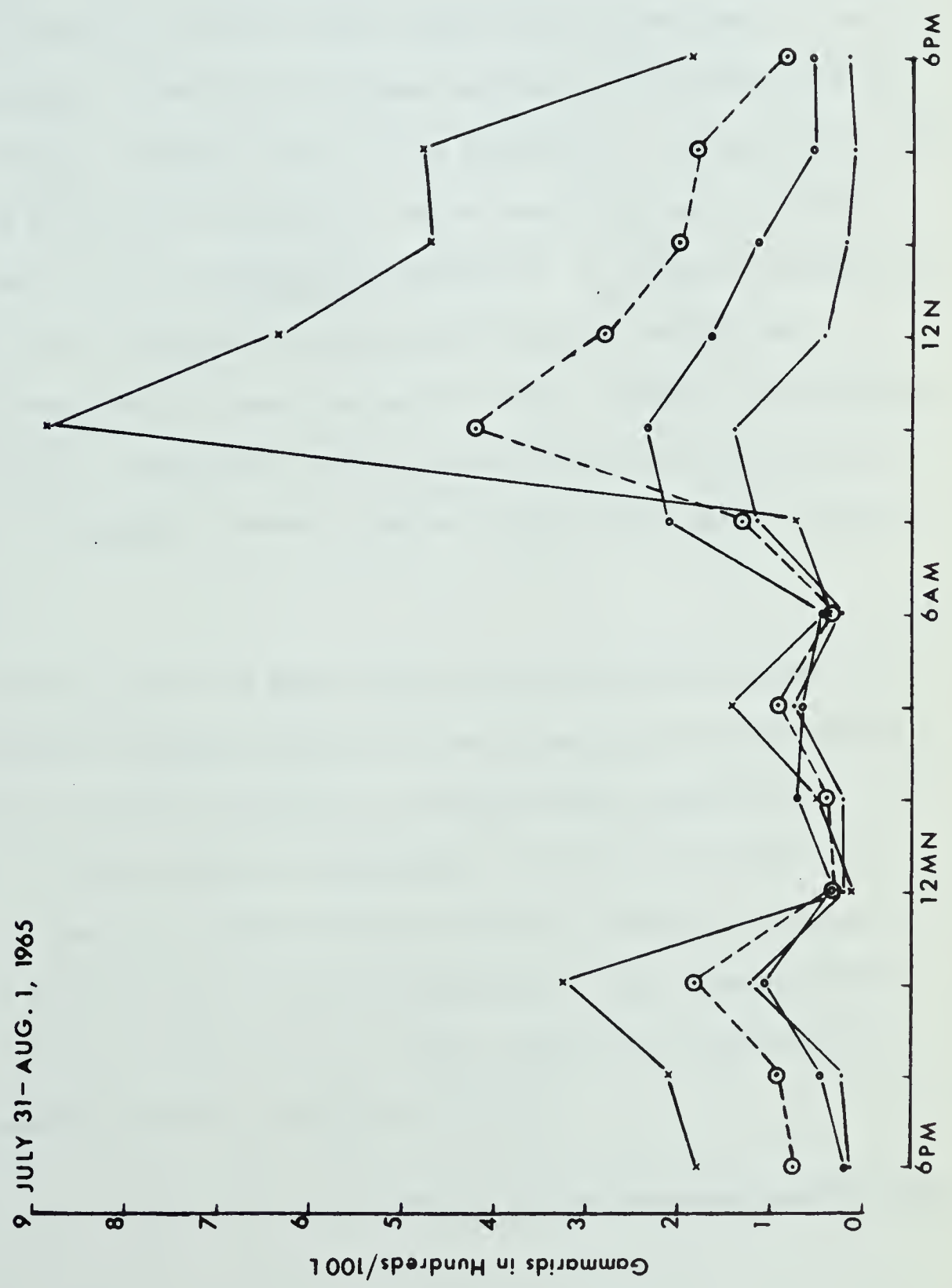
Time					Mean Density
		Surface	Middle	Bottom	
July 31	6 PM	17.5	18.5	183.5	73.16
	8 PM	24.0	49.0	211.5	94.83
	10 PM	122.5	107.0	324.0	184.50
	12 Mdnt.	20.5	31.5	18.0	23.33
Aug. 1	2 AM	22.0	74.0	50.0	48.68
	4 AM	79.0	65.5	145.0	96.50
	6 AM	24.5	44.5	46.0	38.33
	8 AM	119.0	212.0	77.0	136.00
	10 AM	143.5	234.0	888.5	421.83
	12 Noon	45.0	168.0	635.5	282.83
	2 PM	20.0	117.0	473.0	202.33
	4 PM	12.5	52.5	478.5	181.16
	6 PM	18.5	57.0	187.5	87.66

observed. At this time the density of population at all levels, surface, middle and bottom layers, was on the increase. From 2 PM onwards the reverse trend was observed and at 6 PM the original level was attained. The smallest peak observed at 4 AM may also indicate a period of activity at dawn in response to increasing illumination. But the low numbers observed at 6 AM indicate that this was a period of rest when not many were observed

Figure 4. Twenty four hour vertical distribution of gammarids in the three different layers of the open lake as observed on July 31 - August 1, 1965.

Open Lake :
 . Surface
 • Middle
 x Bottom
 ⊙ Mean

FIG. 4



swimming.

From these observations, it is suggested that Gammarus lacustris has a certain diel activity rhythm which accounted for the variations in population density in the open lake. The animals were most active during the day-time between 8 AM and 12 Noon, when they cruised about in the lake. The minimum abundance in the open lake during the dark hours of the night probably indicated that at this time much of the population from the open lake had shifted towards the shore where they sought shelter between cattails and the Potamogeton vegetation. A positive statement to this effect is not attempted as collections from the cattail and Potamogeton areas were not made during the night. However, observations on Gammarus kept in laboratory aquaria, also showed increased activity during hours of daylight, between 8 AM and 12 Noon; and lesser activity in the night.

At present it cannot be said whether these horizontal shifts in population density are manifestations of an endogenous activity rhythm or if they are purely a response to the prevailing conditions of illumination. Factors such as temperature, pH, and O_2 concentration showed little variation during the period of this study, and may not be causative in inducing this horizontal migration. More investigations have to be carried out before we can fully explain this interesting aspect of gammarid behavior in Big Island Lake.

Statistical analysis was not attempted as the data were insufficient.

V. LIFE CYCLE

Sexual dimorphism

The sexes are separate in G. lacustris as in other species, and can be easily distinguished in adults. The male is larger in size, the body length being 2 mm greater than the body length of the female of the same age. The second antenna, shorter than the first in both sexes, is relatively longer and stouter in the male than in the female. A more distinctive character of the male is the presence of calceoli (Fig. 5). These are small transparent globular structures, located on the upper margin of the distal end of the terminal segments of the many jointed flagellum of the second antenna. Calceoli are considered to be chemoreceptors concerned with sex-recognition. Though calceoli have been observed in many species of gammarids, their occurrence as a specific character of the male is reported for some species like G. duebeni, G. minus (Bousfield, 1958) and G. bousfieldii (Cole and Minckley, 1961). An unusual lack of calceoli in males of G. minus has been reported by Cole and Minckley under situations where this species is found in association with G. bousfieldii in the same habitat. However, the presence of calceoli in G. lacustris was found to be consistent and most reliable for purposes of sex distinction.

The locations of genital openings are different in the two sexes. In the female the oviducal apertures are located at the bases of the 5th pair of peraeopods, while in males, the vasa deferentia open at the tips of a pair of distinct tubercles, the genital papillae, present at the bases of the 7th pair of peraeopods (Fig. 6). The palmar of the propodus of the second gnathopod is somewhat concave and oblique in the male whereas in the female it is convex (Fig. 5).

A distinctive character of the mature females is the presence of the

Figure 5. Gammarus lacustris. Diagrams showing secondary sexual characters in adult male and female.

Abbreviations:

a_1 = antenna 1

a_2 = antenna 2

c = calceoli on flagellum of antenna 2 in male

pp = unmodified propodus of gnathopod 2 in female

$pp(g_2)$ = modified propodus of gnathopod 2 in male

FIG. 5

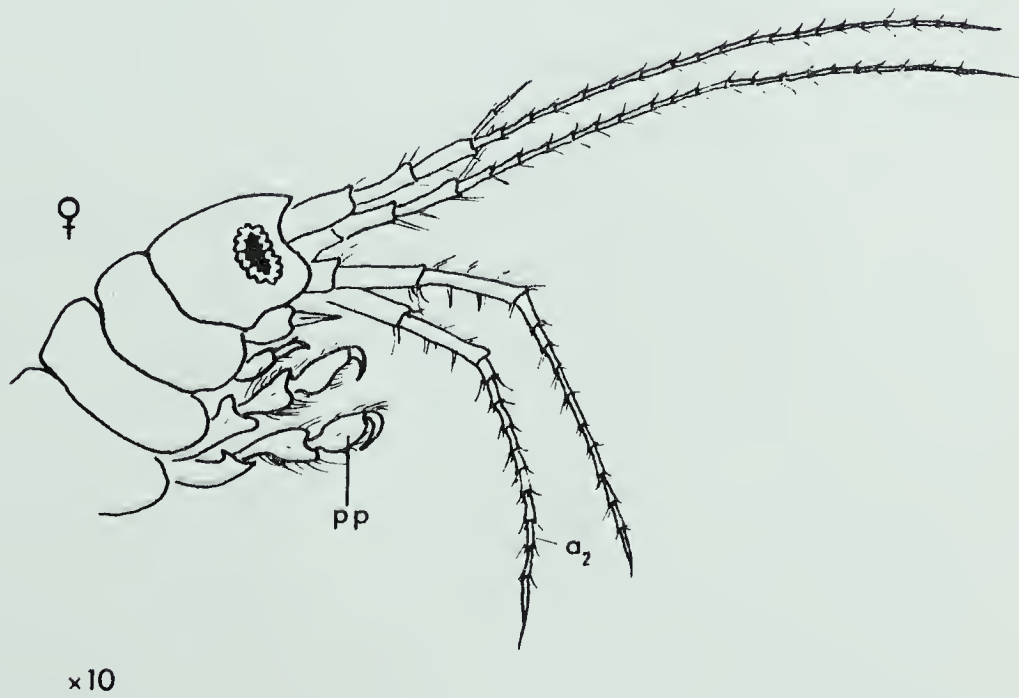
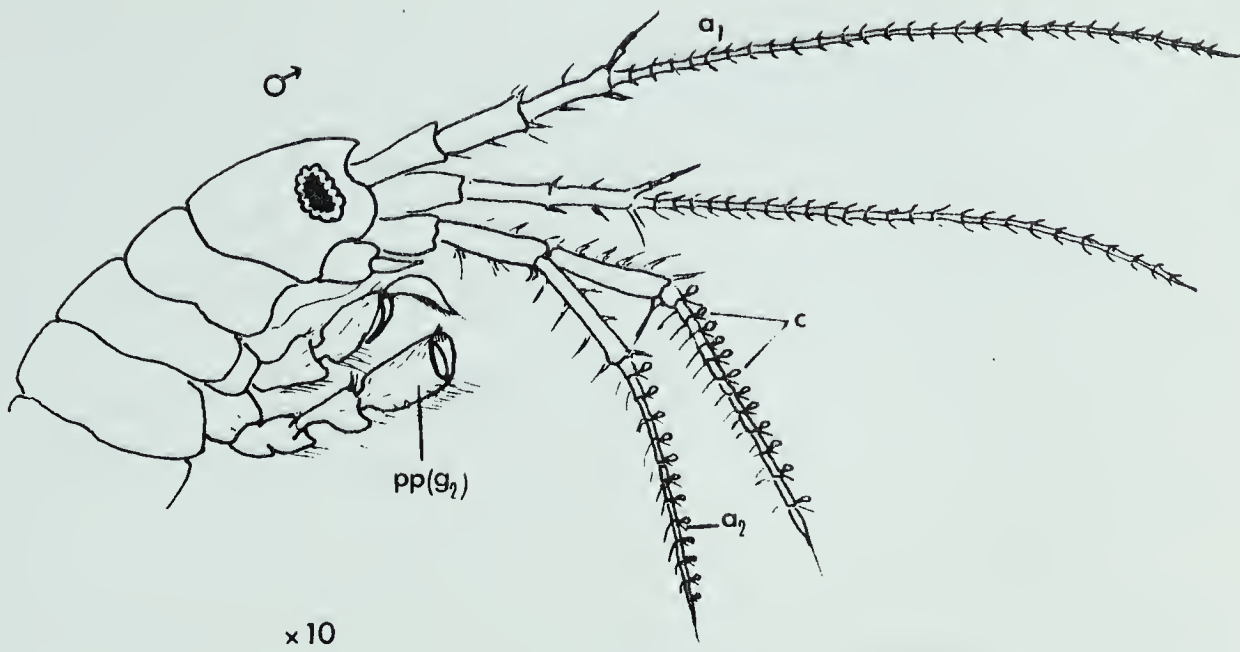


Figure 6. Gammarus lacustris. Male. 7th peraeonic segment showing genital papillae.

Abbreviations:

b = branchia

gp = genital papilla

mgp = male genital pore

p₇ = peraeopod 7

st = sternum

t = tergum

FIG. 6

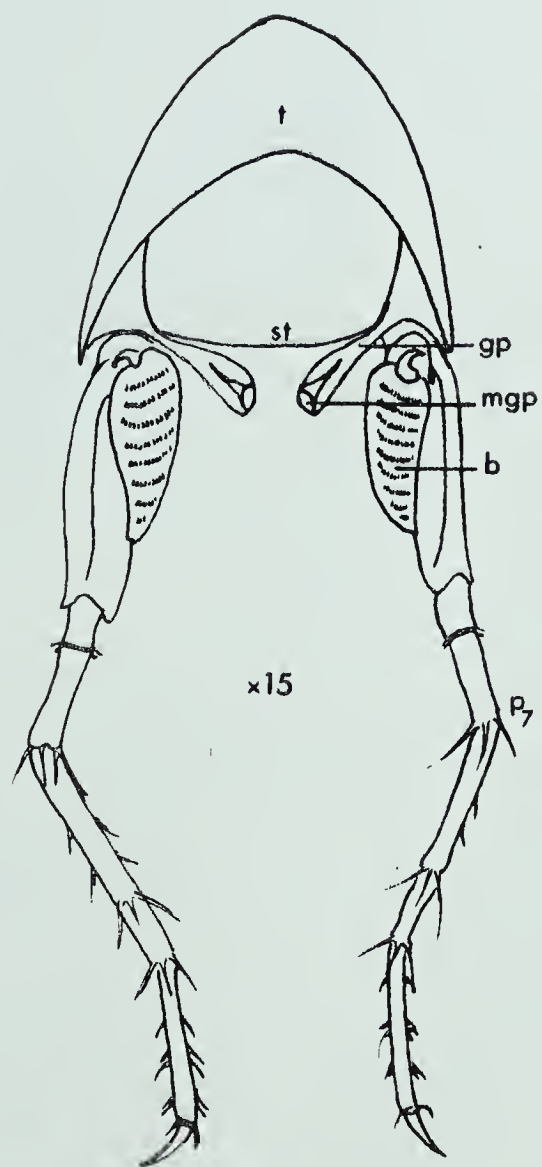


Figure 7. Gammarus lacustris. Diagrams of oostegite in female.

Top left: 2nd peraeonic segment showing arrangement of oostegites forming the brood pouch

Top right: flattened view of fully developed oostegite with marginal bristles

Bottom left: inner view of oostegite in relation to branchia

Bottom right: rudimentary oostegite in juvenile female.

Abbreviations:

bc = body cavity;

os = oostegite;

br = branchia;

r.os = rudimentary oostegite;

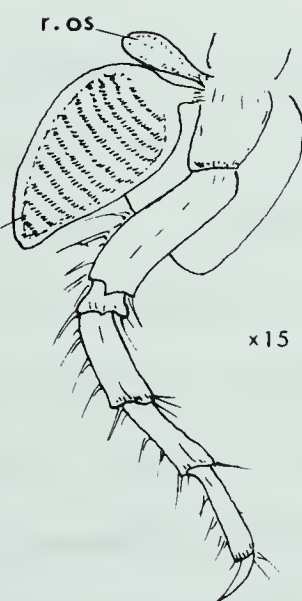
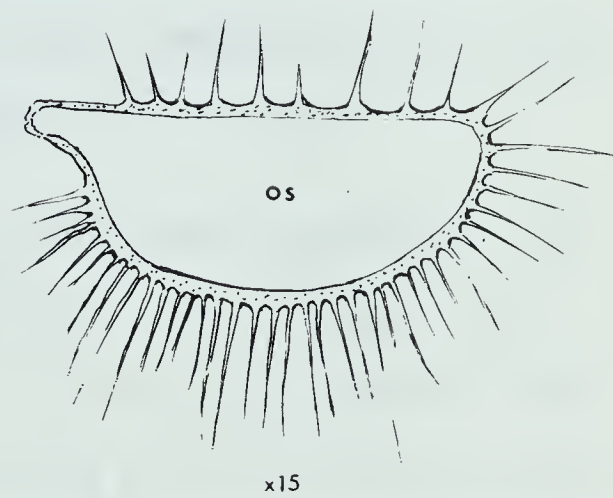
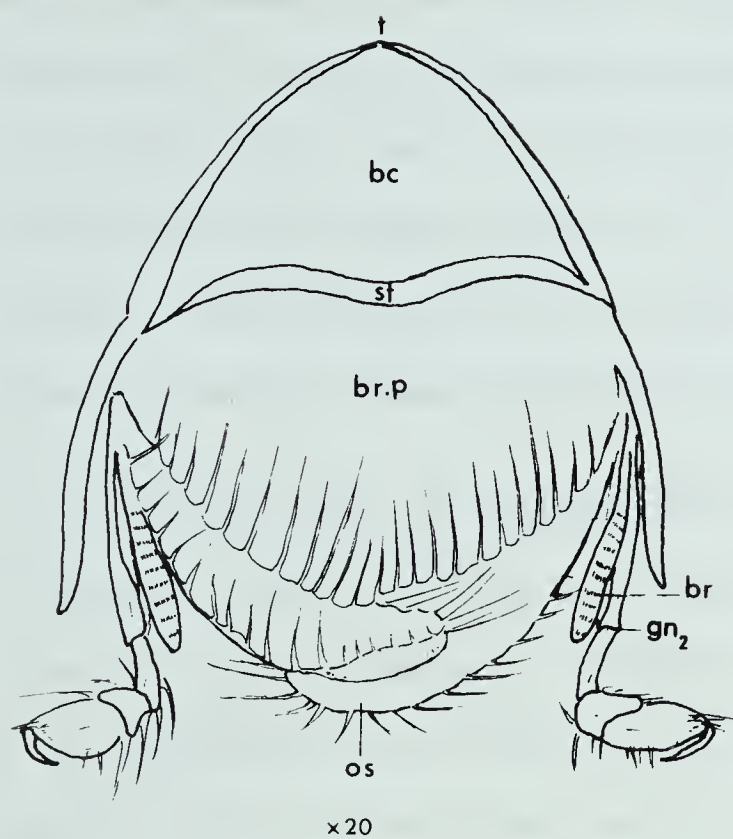
br.p = brood pouch;

st = sternum;

gn₂ = gnathopod 2;

t = tergum.

FIG. 7



oostegites which form the ventral brood pouch during the breeding season. There are 4 pairs of oostegites associated with the 2nd, 3rd, 4th, and 5th pair of pereopods. Each oostegite is a thin flexible lamella, somewhat elliptical in outline, arising internally, basal to the branchia (Fig. 7). In the final moult, prior to oviposition, the oostegite acquires a set of long bristles all along the border. The fully formed oostegites are obliquely laid one across the other with their terminal ends overlapping so as to form the compact brood pouch. (Fig. 7)

The sexes cannot be distinguished in the immature gammarids. But, in juveniles, which are more than 2 months old, the secondary sexual characters begin to appear as rudiments. In the males, calceoli appear on the flagellum of the second antenna, along with the rudimentary genital papillae on the ventral side, and in the female rudimentary oostegites begin to appear (Fig. 7). Thus on the basis of these characters, sexes are distinguishable from the time gammarids are two months old.

Precopula

The onset of reproductive activity was marked by the pairing of the two sexes which occurred in early spring soon after the ice-thaw. The male held on to the female by hooking the claws of its first gnathopod below the front end of the first segment of the pereopod of the female. Occasionally the second gnathopod was also used for a stronger hold. In this condition, the couple swam together, often for days until ovulation was completed. Though precopula generally occurred prior to ovulation, it was common to see such pairs during the winter months, which only showed that precopula may occur far ahead of ovulation, when the individuals were mature and receptive, but not yet ready for ovulation, as they were still in their penultimate instar.

The final moult prior to reproduction occurred only after the ice-thaw. At this time males moulted earlier than females in readiness for the breeding activity. While most females had entered precopula just after the final moult, some were seen to moult while in precopula. The male used its first and second gnathopods interchangeably, and never lost grip of the female, while the female crept out of its moult. With the final moult, the brood pouch was fully formed in the female. The female had to be freshly moulted for oviposition, copulation, and fertilization, which had to be gone through before the integument was hardened. The "precopulatory grasp" continued for a short while after ovulation when the two sexes separated. The females resisted any further mating until the first brood was released from the brood pouch.

Fertilization

Fertilization is external. As ova are released into the brood pouch through the softened oviducal apertures, fertilization is accomplished by the ejection of sperm masses through the genital papillae of the male. The subsequent transference of sperms along with the water current was effected by the first pair of unmodified pleopods in the male. During copulation, the male assumed an oblique position, without losing hold of the female, to bring the genital papillae in line with the ventral brood pouch of the female.

Fecundity

As described by Allee et al. (1949), fecundity refers to egg production, and fertility refers to the number of eggs that develop into the living young. Both these attributes could be clearly followed in G. lacustris. During the breeding season, the numbers of eggs borne by gravid females were counted regularly. In the months of May and June when all the females

were bearing the first brood, the mean number of eggs per female was 32.5, while in July, when the surviving females had a second brood, the mean number of eggs per female was only 21.5 (Table 4 and Fig. 8).

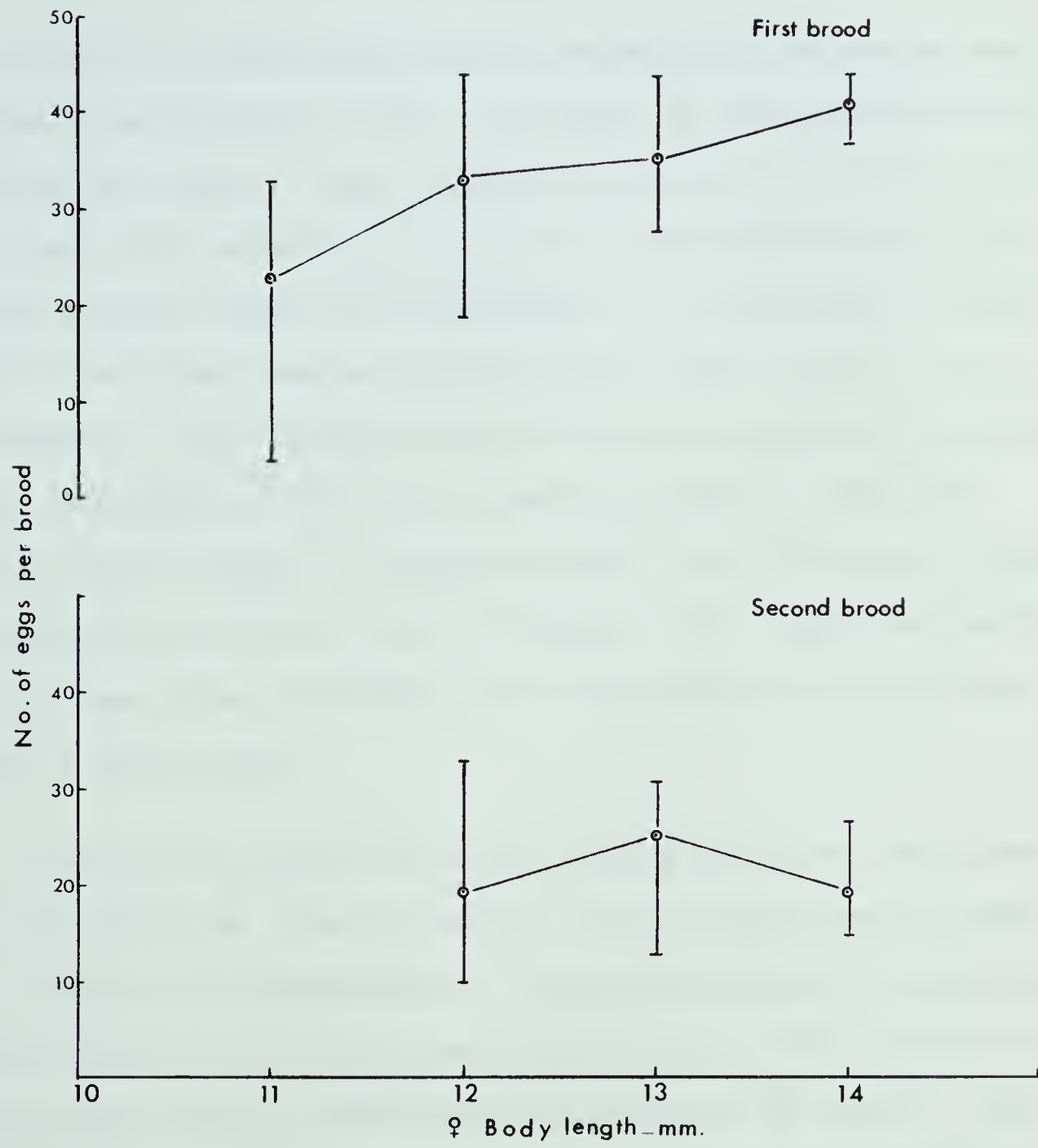
Table 4. Body Length of Female and Seasonal Fecundity

	First brood				Second brood		
	1965						
	May 12 - June 15				July 5 - July 21		
Body length in mm.	11	12	13	14	12	13	14
No. of eggs per female	26	44	28	40	28	27	27
	4	39	44	42	33	28	12
	18	31	42	39	14	13	16
	25	38	40	45	21	27	24
	15	19	30	43	17	24	20
	33	37	33	44	16	31	17
	21	36	37	42	18	30	21
	20	26	36	38	10	22	18
	18	27	32	37	24	24	15
	23	33	33	40	14	30	26
Mean no.	20.3	33.0	35.5	41.0	19.5	25.6	19.6
Seasonal mean	32.45				21.56		

It was also observed that the initial number of eggs produced by the females varied according to their body length. Eleven-millimeter individuals produced on the average 20.3 eggs, 12 mm. individuals 33.0 eggs, 13 mm. individuals 35.5 eggs, and 14 mm. individuals 41.0 eggs. Such a relation

Figure 8. Gammarus lacustris (female). Mean brood size
with range in vertical lines.

FIG. 8



between the size of female and the number of eggs in the brood pouch has been observed in other amphipods. (Cheng, 1942; Clemens, 1950; Kinne, 1952; Hynes, 1954; and Kinne, 1960 and 1961).

However, the same relation was not evident when the females were bearing a second brood in July. As a result of the intervening moult, the three size classes 11 mm., 12 mm., and 13 mm., had shifted to the next higher size classes of 12, 13, and 14. The earlier set of 14 mm. females were not observed in later samples. The mean number of eggs was 19.5 for 11 mm. females, 25.6 for 13 mm. females and 19.6 for 14 mm. females. Thus taking count of the two broods produced by the female, 12 mm. individuals of the initial breeding population produced the maximum number of eggs (58.6 eggs per female), since the 14 mm. individuals did not bear a second brood. Similarly 13 mm. individuals produced only 39.8 and 14 mm. individuals only 41 eggs, as they were not found to bear a second brood.

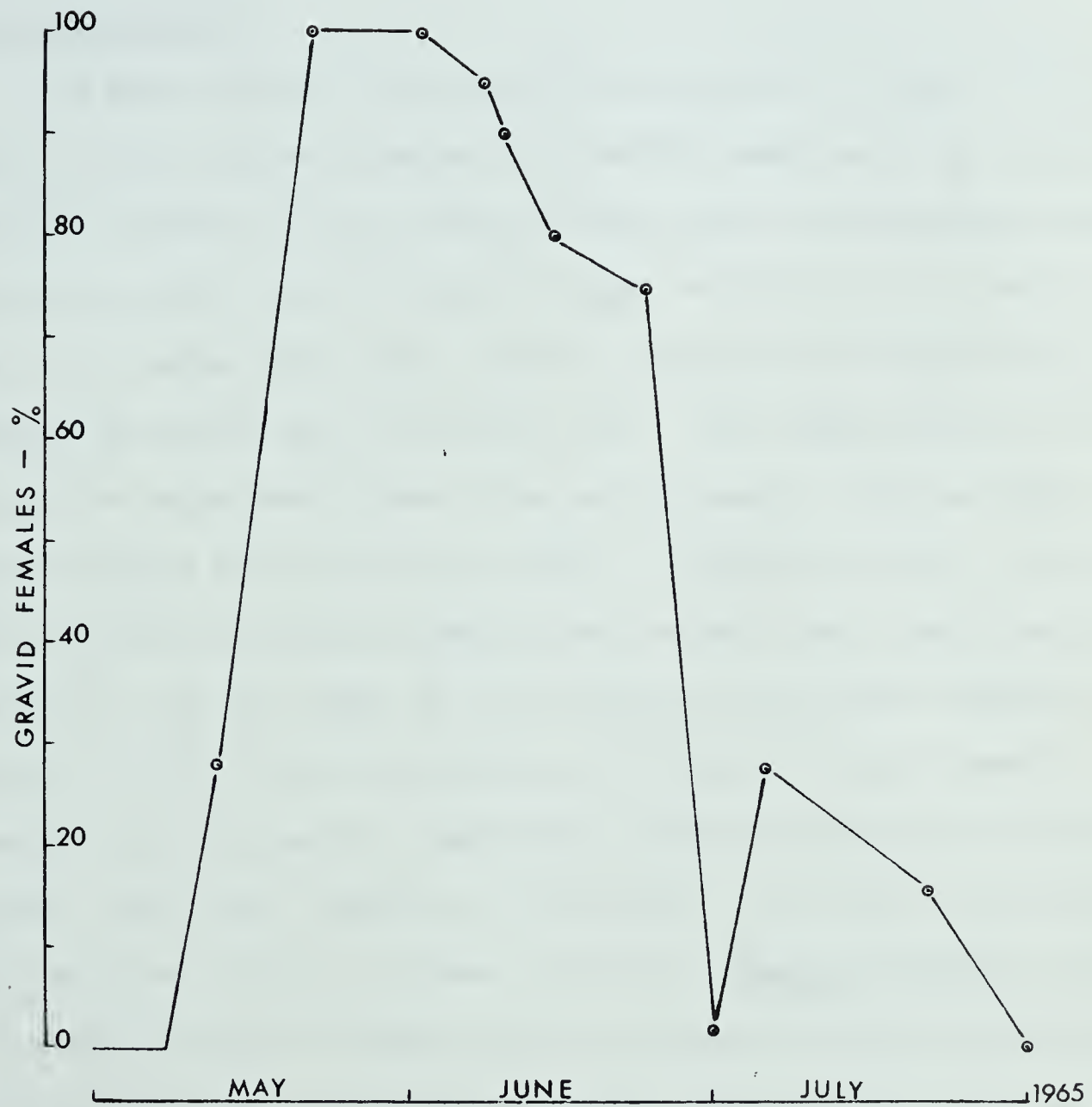
Fecundity, in terms of the whole breeding population, was highest in the 12 and 13 mm. class of females, and the preponderance of these size classes at the commencement of breeding was definitely advantageous to the population considering their ability to reproduce a second time, and the total number of immatures recruited within the period. Figure 9 shows the percentage of gravid females observed in the population during the entire breeding period in 1965.

Fertility

In G. lacustris, the number of immature individuals released did not differ from the number of eggs present in the brood pouch. Infertile eggs or deformed embryos were not observed and it can be presumed that

Figure 9. Number of gravid females per hundred during breeding season. May through July 1965.

FIG. 9



the mean number of eggs present in the brood pouch represented the number of young hatched. It must be mentioned, however, that a few instances where the development was found to be defective. were cases of heavy parasitic infestation with cestode cysts, while the more common cystacanth infection did not have any ill-effect.

Incubation Period

The time interval between the first appearance of eggs in the brood pouch and the earliest appearance of newborn immatures in the population could be reckoned as the incubation period under the prevailing conditions. In the year 1965, the first batch of eggs were laid into the brood pouch during the second week of May, and the release of immatures started towards the end of the first week in June. This would mean that the total incubation period was between three to four weeks. The mean water temperature during this period was 14.9°C . As compared to this, in the month of July when the surviving females had a second brood, the incubation period was only two weeks, at a time when the mean water temperature was found to be 22.0°C . Thus, the duration of incubation period seems to be considerably influenced by temperature, higher temperatures favoring earlier, more rapid completion of incubation. This was in close agreement with the findings of Clemens (1950) for Gammarus fasciatus, where a similar influence of temperature on incubation time was experimentally demonstrated under laboratory conditions. The recorded incubation periods in G. fasciatus varied from 7 days at a temperature of 24°C . to 22 days at a temperature of 15°C . Kinne (1960 and 1961) has also reported on the temperature effects on the rates of embryonic development in G. salinus and G. zaddachi which were similar.

Depending on the prevailing temperatures, after an incubation period

of two to four weeks the immature gammarids were recruited mostly during the months of June and July. After a period of rapid growth, they developed secondary sexual characters and became mature pre-reproductive adults by October of the same year. In this condition they overwintered without further moulting and growth. Soon after the ice-thaw these individuals moulted and were in precopula. Thus the breeding cycle started in the new generation of reproductive adults after a period of 10 to 11 months. The life cycle in G. lacustris, as observed in the present study was annual.

VI. AGE, GROWTH AND SIZE

The newborn, immature gammarids observed both in the laboratory cultures and in the field, had a mean body length of 2.25 mm. Within the first month of postnatal growth there was almost a twofold increase in body length. Immatures released during the first week of June, attained a mean body length of 5.12 mm. by the first week of July. The second month was also a period of rapid growth, and by the second week of August, the secondary sexual characters were evident and the sexes could be distinguished. At this time the linear difference in growth between males and females was clearly discernible. The males had reached a mean body length of 9.03 mm. while females showed a mean body length of 7.76 mm. Table 5 gives a record of the mean body lengths with the standard deviations and standard errors, with the approximate age indicated in days. In the present description, individuals older than two months are designated as juveniles, when sexes are also distinguishable. From the time the gonads begin to develop, until the onset of breeding season, they are termed the pre-reproductive adults. Thereafter, they are called reproductive adults and post-reproductive adults. The various stages in the life cycle are tabulated separately to show the approximate number of moults against the mean body length (Table 6).

The mean body lengths recorded in Table 5 are based on the measurements made on individuals recruited within a short interval of time (approximately two weeks), and followed over until the onset of winter, by taking frequent samples. With the data obtained, a mass growth curve is plotted as in Figure 10 which shows the growth pattern more clearly.

Table 5. Mean body length of gammarids showing approximate age in days after birth. June - Oct. 1965

Date of Sampling		Approximate age in days after birth	Mean body length in mm.		S D	S E	
June	5	0	2.25				
June	15	9	2.61		0.53	0.19	
June	23	17	3.51		0.68	0.18	
June	30	24	4.35		0.77	0.21	
July	5	29	5.12		0.94	0.18	
July	12	36	5.74		0.99	0.27	
July	15	39	6.41		1.12	0.31	
July	21	45	6.81		1.30	0.36	
			Males Mean	S D	S E	Females Mean	
August	1	56	8.91	1.38	0.38	7.68	1.23 0.34
August	10	65	9.03	1.38	0.38	7.76	1.26 0.34
August	25	80	10.22	1.59	0.44	8.50	1.33 0.21
Sept.	28	113	11.32	1.80	0.49	9.94	1.56 0.43
Oct.	22	137	12.28	1.86	0.52	10.56	1.62 0.45

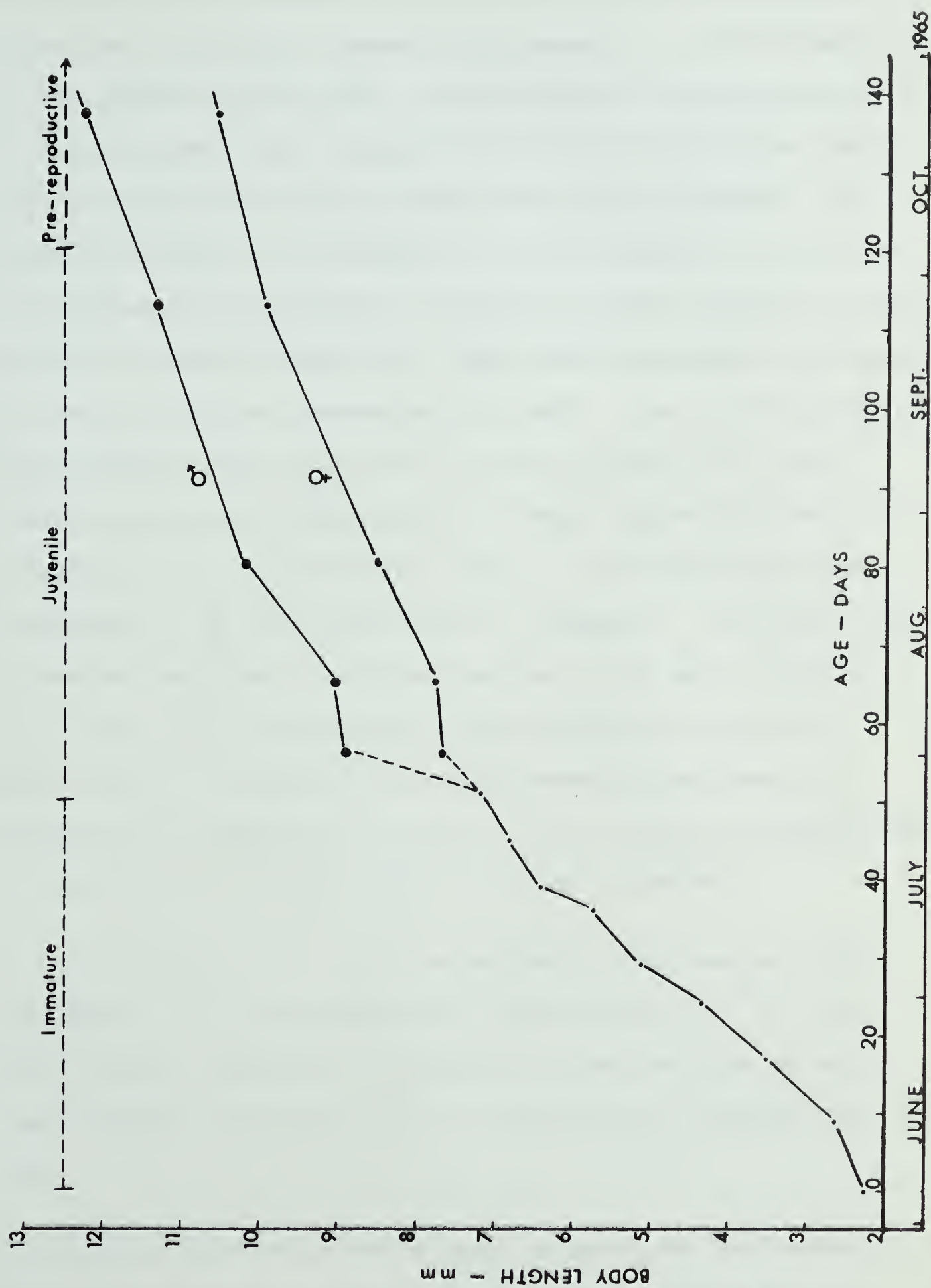
Table 6. Stages in the life cycle of Gammarus lacustris showing approximate number of moults and mean body length in millimeters (mm).

Stage in life	Approximate number of moults	Body length in mm.
Immature	1 to 8	2 to 7
Juvenile	8 to 10	7.5 to 9.5 (female) 8.5 to 10.5 (male)
Pre-reproductive	10 to 13	10 to 13 (female) 11 to 14 (male)
Reproductive	13 to 15	11 to 14 (female) 12 to 16 (male)
Post-reproductive	15 and above	14 to 16 (female) 15 to 20 (male)

The steady and rapid growth during first fifty days of life was followed by a prepubertal moult marked on the growth curve by a change in slope between the 7 and 8 mm. level for female and between 8.5 and 9.5 mm. level for the male. The secondary sexual characters became established during this period. There was a cessation of growth with a long intermoult period of approximately three weeks, when the mean body lengths of both male and female remained more or less the same. There was also a general slowing down of the growth rate in the subsequent period with corresponding increase in the intermoult period. This was also a time when the decreasing trend in water temperatures was noticed. On August 25, gammarids which were approximately 80 days old showed a mean body length of 10.22 mm. for males and 8.5 mm. for females. By September 28, when the age had increased by one month, the body length showed only

Figure 10. Mass growth curve. based on measurements of mean body length of fifty gammarids from the time of birth until 140 days of age. Male and female body lengths are plotted separately from the time sexes are distinguishable. (June to October 1965)

FIG. 10



an increase of a little over 1 mm., the mean body length of males was 11.32 mm. and of the females was 9.94 mm. Within the next one month period, the first batch of gammarids approximately in their 5th month of life, became sexually mature. Ovaries appeared in the females as two distinct dark bands, on either side of the mid-dorsal line, which could be observed through the somewhat transparent integument. The testes in the males also developed in the same position, but could not be recognized unless dissected, as they had the same translucent appearance as the digestive diverticula. Such individuals which had developed the gonads, formed the pre-reproductive adults. Thus the development of gonads occurred before the onset of winter conditions in the lake, though the final moult during which the female acquired bristles on the oostegites did not occur until the spring. The overwintering stage corresponded to the penultimate instar. Throughout the winter months no breeding took place, though the readiness of the male to copulate was evident from the precopula observed occasionally during the winter months. Cessation of growth, and consequent suppression of breeding were all observed in relation to the prevailing low temperatures, low oxygen content, and the effects of winter stagnation.

The mean body length of the overwintering adults was very much influenced by the total growth period they experienced in the lake prior to winter stagnation. A comparison of the overwintering adults from 1964-1965 winter months with the 1965-1966 winter samples made this clear.

In 1964, there was an earlier onset of spring and the ice-thaw occurred by the middle of April. Breeding commenced early and the mean body length of juveniles on July 21, 1964 was 7.42 mm. In 1965,

breeding was delayed as the ice-thaw did not occur until the first week of May, and the juveniles of July 21st, 1965 measured only 6.8 mm. This difference in growth was still more apparent in the October samples of the two years. In 1964, the pre-reproductive adults of the newly recruited population had a mean body length of 13.4 mm. for males and 10.88 mm. for females, while in 1965, males measured only 12.28 mm. and females, 10.46 mm. Likewise an earlier onset of winter, or cold spells during the fall may also retard the growth rate which would be reflected in the mean body length values of the overwintering adults.

The slight fluctuations in mean body lengths of males and females observed in the winter samples, can be partly explained on the basis of the differential mortality of the different size classes. Moreover, the first and second batches could be distinguished only during the first three months of their life. The rapid growth during the early instars, with subsequent slowing down of the growth rate in later instars, gave time for the second batch to catch up with the first, with the approximation of body lengths. This made it difficult to distinguish the two batches in the winter samples, and the two sets were treated together while taking body length measurements.

In the month of May 1965, after the overwintering period, both males and females moulted prior to breeding. The mean body length of the males increased to 15.64 mm. from 13.9 mm. observed in March, and in the females the mean body length increased from 11.32 mm. to 12.48 mm. These breeding adults were approximately 10 to 11 months old, which was the normal reproductive age. Though many males moulted after the precopula and copulation, the females never moulted while they carried the brood. After the release of the brood, most females died,

having completed the average span of life, 12 to 13 months. The surviving males and females had mean body lengths of 14.94 mm. and 12.78 mm. respectively, as observed on July 21, when the surviving females were bearing their second brood. By the first week of August, the release of the second batch of immatures was completed, and the few surviving members of the parent population constituted the post-reproductive adults, with mean body lengths of 15.6 mm. in males and 13.5 mm. in females, as was observed on August 25, 1965. Some of these post-reproductive adults were present in the winter samples of 1965-1966. These were individuals surviving beyond the average life span of 13 months, and some of them at least could realize their maximum longevity of two years. The unusually large individuals measuring 18 to 20 mm. in body length, observed in the early spring catch of 1965, represented such two-year-olds. Being senile they were soon eliminated from the population due to natural mortality.

VII. POPULATION STRUCTURE

The following description is a monthly statement of the population structure of Gammarus lacustris in Big Island Lake, for the whole year 1965, January to December, based upon the percentage distribution of the various size classes. These are shown in Figures 11, 12, 13, and 14. The samples taken during the months of January, February, and March in 1966, have also been taken into account for the sake of comparison, with the corresponding winter population of 1965.

January 1965Table 7. Percentage composition of Gammarus population.

January 1965 and 1966

	Jan. 16, 1965			Jan. 11, 1966		
	Pre-repro- ductive	Juveniles	Total	Pre-repro- ductive	Juveniles	Total
% of	63	-	63	63	4	67
size range in mm.	13 - 16	-		11 - 17	10	
% of	37	-	37	22	11	33
size range	10 - 13	-		10 - 13	8 - 9	
Total	100		100	85	15	100

The structure of the overwintering Gammarus population almost exclusively composed of pre-reproductive adults, revealed a proportion of 63% males to 37% females. This change of sex ratio in favor of males was also observed during the subsequent winter months. The body lengths

Figure 11. Percentage composition of Gammarus population samples showing size and sex distribution. Vertical scale gives the body length in mm. and horizontal scale gives the percentage frequency. Males are shown to the left and females to the right of the broken vertical line. January, February, and March 1965 and 1966.

FIG. 11

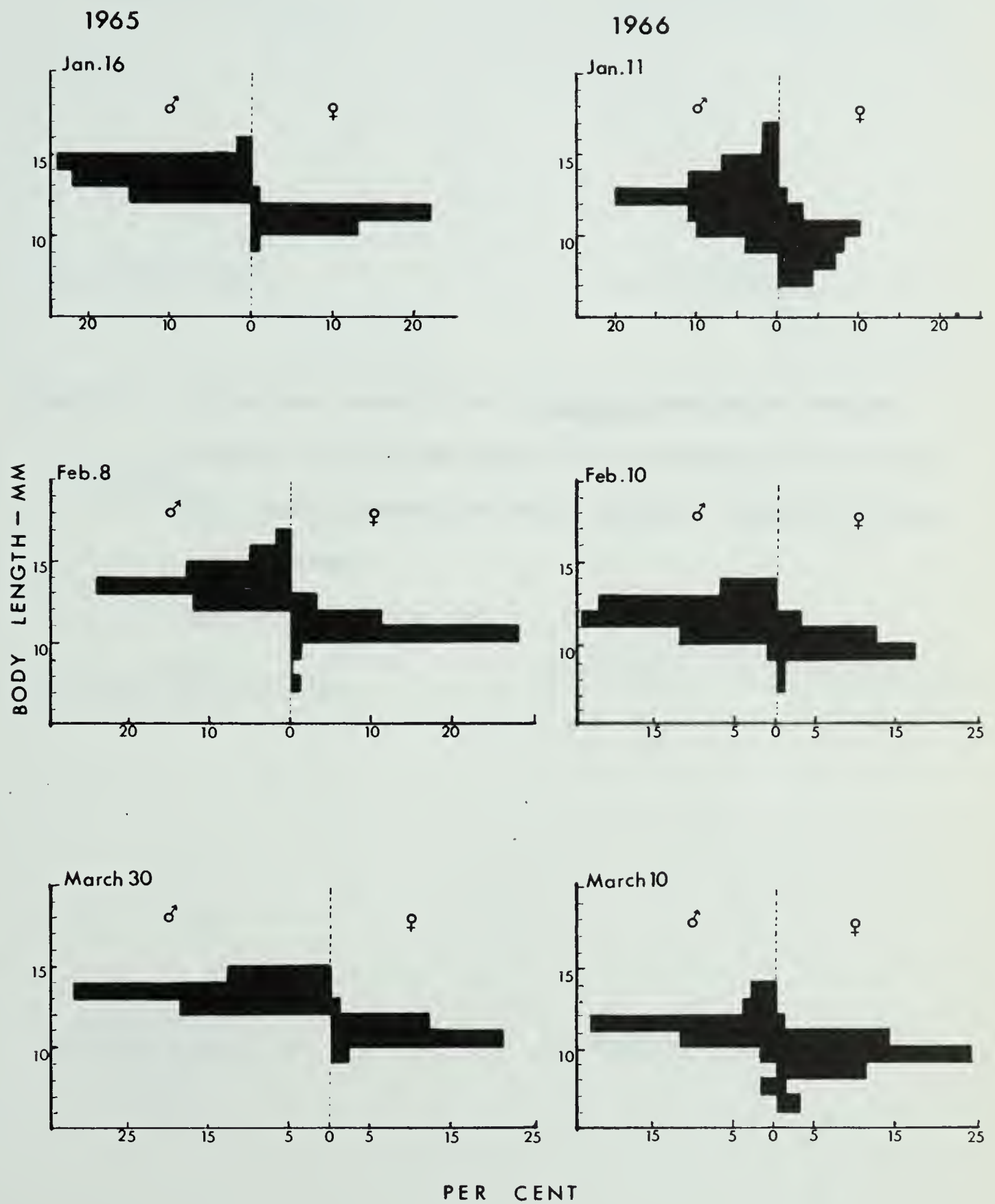


Figure 12. Percentage composition of Gammarus population samples showing size and sex distribution, arranged as in Figure 11. Gravid females are shown stippled. Immature stages are centered.

May, June and July 1965.

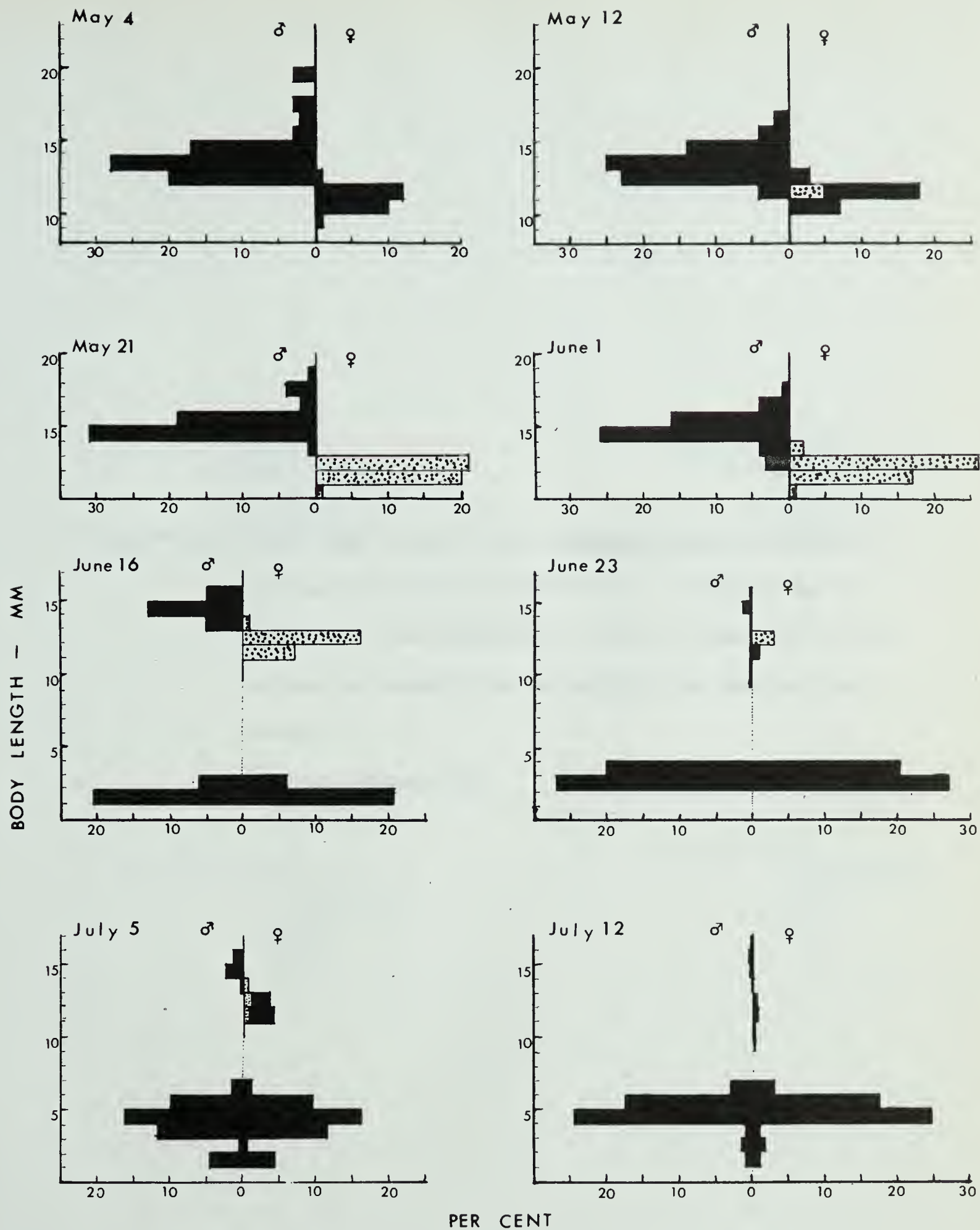


Figure 13. Percentage composition of Gammarus population samples showing size and sex distribution. Arranged as in Figure 11. Sex distinction level is indicated by the horizontal broken line below which the immatures are centered.

July and August 1965.

FIG. 13

1965

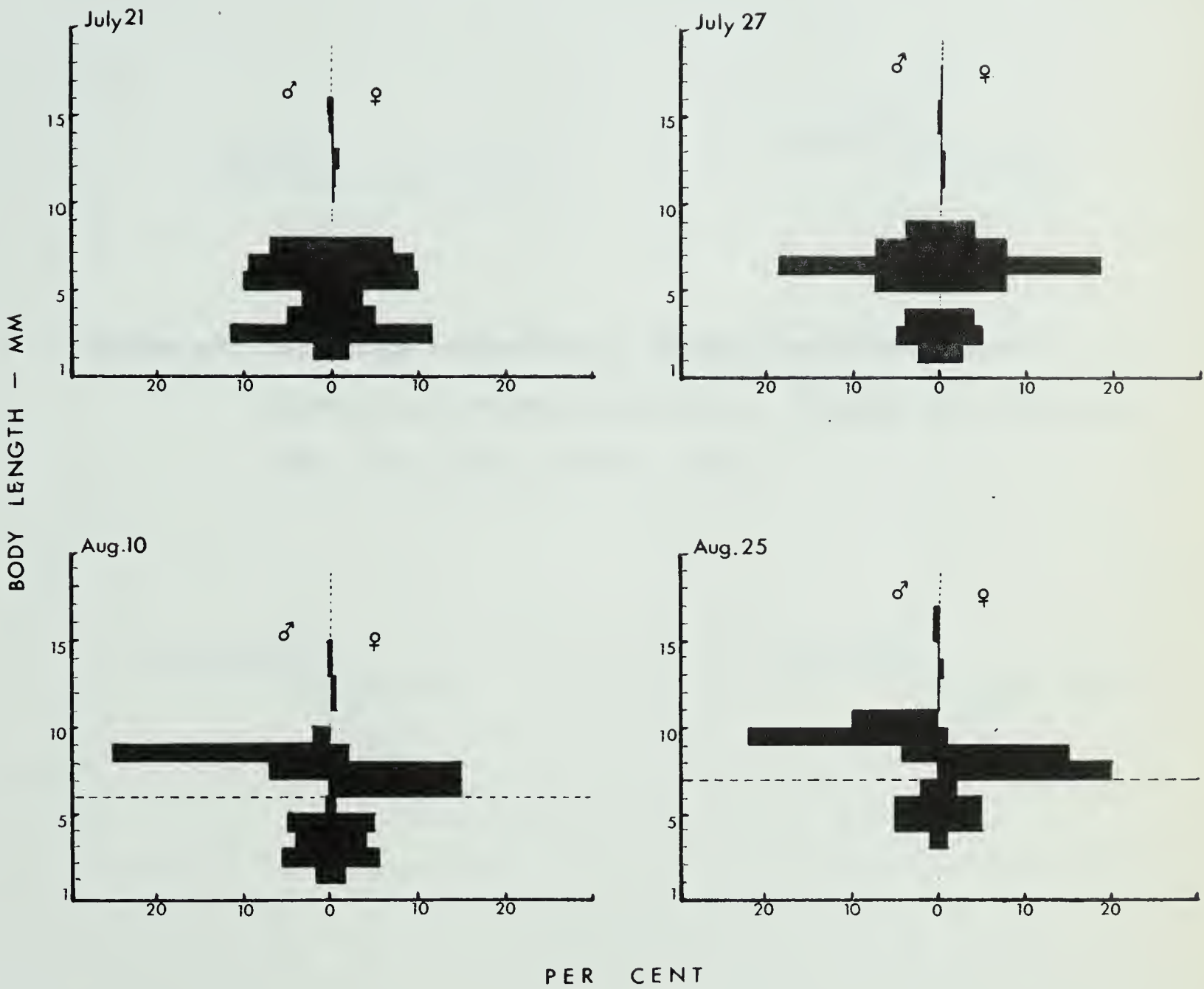


Figure 14. Percentage composition of Gammarus population samples showing size and sex distribution. Arranged as in Figure 13. Sept., Oct., Nov., and Dec. 1965.

FIG. 14

1965

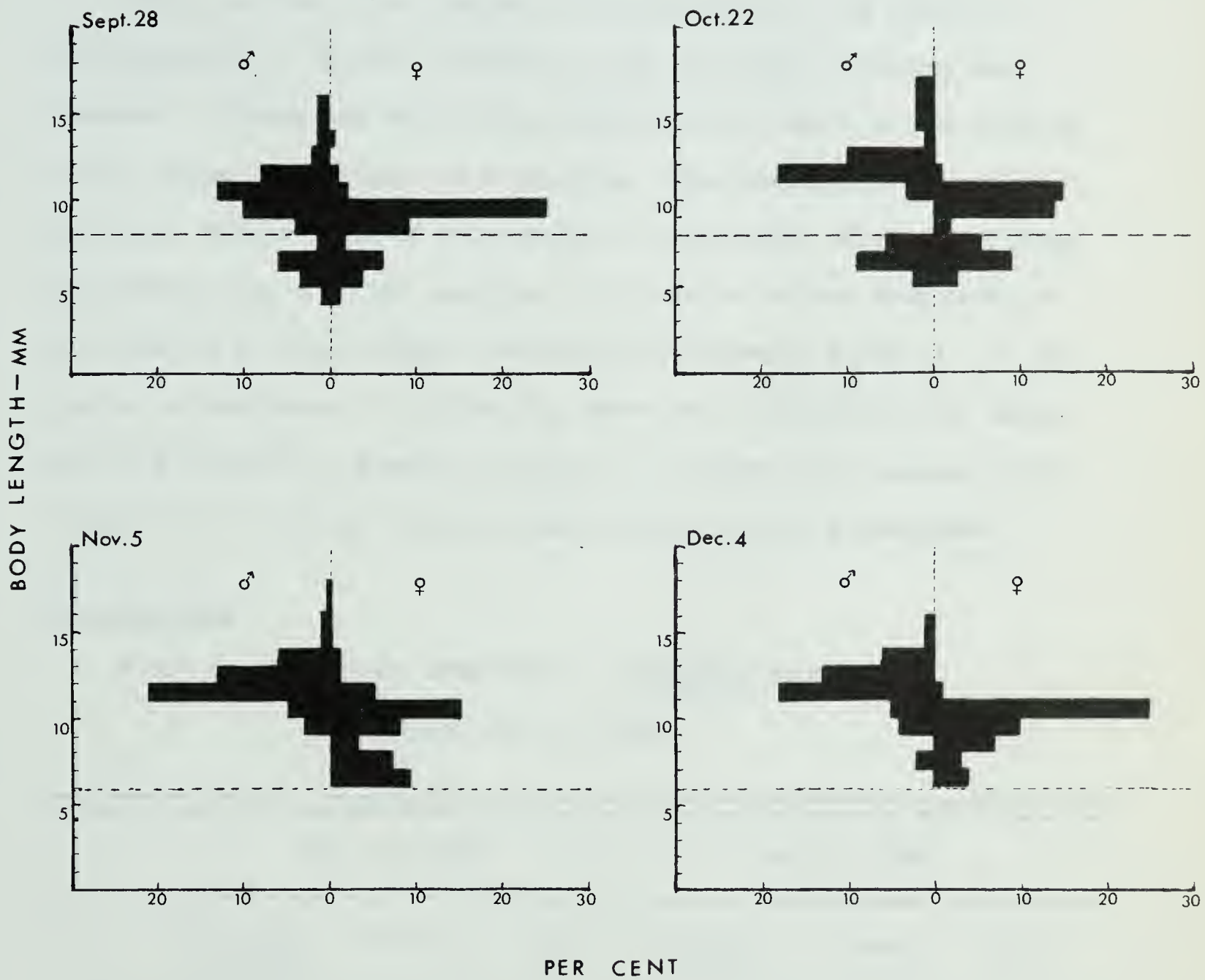




Figure 1

varied from 13 to 16 mm. in the males and 10 to 13 mm. in the females. Juveniles were absent.

In comparison, the 1966 sample was somewhat different. Though the overall sex-ratio was similar, with 67% males and 33% females in the population, a greater variation in the size-class frequency was observed. Fifteen per cent of the population were still in the juvenile stage, having body lengths of 8 to 10 mm. This variation was partly due to an earlier spell of cold weather in 1965-1966, which slowed down the growth rate. At the same time, the onset of winter conditions in the lake was also slow, which resulted in the greater survival of the smaller size-classes. In 1964-1965, there was a sudden onset of winter, and this resulted in greater mortality of the lower size classes, which accounted for the more restricted distribution of the size-classes.

February 1965

Table 8. Percentage composition of Gammarus population.

February 1965 and 1966

	Feb. 8, 1965			Feb. 10, 1966		
	Pre-repro- ductive	Juvenile	Total	Pre-repro- ductive	Juvenile	Total
% of male	56	-	56	65	1	66
size range in mm.	13 - 17			11 - 14	10	
% of female	43	1	44	32	2	34
size range in mm.	10 - 13	8		10 - 12	8 - 9	
Total	99	1	100	97	3	100

The February population showed 56% males and 44% females. The variation in sex-ratio was due to differential mortality of the two sexes. As far as the males were concerned, the same size classes, 13 mm., 14 mm., and 15 mm., were observed, while among the females the larger size class of 12 mm. individuals were reduced in number. Sixty-four per cent of the females belonged to the 11 mm. size class.

In February 1966, the population was composed of 66% males and 34% females.

The mean body length of males was 12.3 mm. and of females was 10.4 mm. as compared to 14.2 mm and 11.3 mm., the corresponding figures for February 1965. The slower rate of growth seen in 1966 was also evident from the fact that the largest males and females measured only 14 mm. and 12 mm., respectively, while in February 1965, the largest males measured 17 mm., and females 13 mm.

March 1965Table 9. Percentage composition of Gammarus population.

March 1965 and 1966

	Mar. 30, 1965			Mar. 10, 1966		
	Pre-repro- ductive	Juvenile	Total	Pre-repro- ductive	Juvenile	Total
% of ♂	64	-	64	42	4	46
size range in mm.	13 - 15			11 - 14	8 - 10	
% of ♀	36	-	36	50	4	54
size range	10 - 13			10 - 12	7 - 8	
Total	100		100	92	8	100

During March significant shifts in population structure occurred due to the mortality caused by the adverse effects of winter stagnation. This was a time when anoxic conditions prevailed and hydrogen sulphide was found to be present. Heavy mortality was experienced by the population apparently affecting all age groups. But, the surviving population of resistant individuals was found to be composed of 13 mm., 14 mm., and 15 mm. size classes of males forming 64%, and 10 mm., 11 mm., 12 mm., and 13 mm., size classes of females forming 36% of the population.

The elimination of larger 16 and 17 mm. males brought down the mean body length of males to 13.9 mm. from 14.2 mm. observed in February 1965, whereas among females, the smallest size classes of 8 mm. individuals were absent, and a few of the 13 mm. individuals also were eliminated, and the mean body length remained the same at 11.3 mm.

In contrast, during March 1966, more females were present constituting 54% of the population. The size-class structure also was different. Females varied in body length from 7 mm. to 12 mm., while males varied from 8 mm. to 14 mm. Though the two populations of March 1965 and March 1966 were not different in age, the observed differences in the size classes were brought about by the slower growth rate, and the greater survival of the second batch of juveniles in 1966.

April 1965

Sampling was not attempted in the lake during this month as the ice-cover had become soft. However, it was presumed that the conditions were similar to those in March, except that the ice-thaw began during the second half of this month.

May 1965

Table 10. Percentage composition of Gammarus population.

May 1965

	May 4			May 21		
	Post-repro- ductive	Repro- ductive	Total	Post-repro- ductive	Repro- ductive	Total
% of ♂	3	73	76	-	58	58
size range in mm.	20	13 - 18			14 - 19	
% of ♀	-	24	24	-	42	42
size range in mm.		10 - 13			11 - 13	
Total	3	97	100		100	100

The first sample for the spring of 1965 was collected on May 4, almost a week after the lake was completely clear of ice. This sample could be considered representative of that section of the overwintering population which had successfully gone through the rigors of winter stagnation. As observed during the winter months of 1964-65, the sex ratio was heavily in favor of males, the females formed only 24% of the population. All the females came within the size classes of 10 to 13 mm., while the males were found to vary in body length from 13 to 18 mm.

Though the majority of males was in the size classes 13, 14, and 15 mm., about 8% of the population, all males, were in higher size classes of 16, 17, and 18 mm. This showed that some males had already moulted ahead of the females in preparation for the breeding activity. The few unusually large males, which measured 20 mm., were the survivors of the original parent population, post-reproductive adults, which had almost reached their maximum life span of two years. Such individuals formed only 3% of the population and did not appear in subsequent samples, as they were soon eliminated from the population.

From May 4 to May 21, the rapid increase in the 12 and 13 mm. size class of females, and the 15 and 16 mm. size class of males marked the completion of the final moult and the almost synchronous onset of the reproductive period in the population. Gravid females were first observed on May 12 (shown stippled in figures), when 8% out of the total 28% female population had eggs in their brood pouch. By May 21, the whole female population had completed ovulation (Fig. 9). As these reproducing adults were recruited into the population during the previous spring, in the months of May and June, 1964, the reproductive age of these individuals

was 11 to 12 months.

The frequency distribution as seen on May 21 (Fig. 12) was characteristic of the breeding population. The gravid females had a mean body length of 12.4 mm. and the males had a mean body length of 15.6 mm. Males constituted 58% of the population and females 42%.

The rapid decrease in the male section of the population was mainly due to the mortality experienced by the males at the beginning of spring and following an active period of precopula. Thus, within a period of two weeks, from May 4 to May 21, a wide shift in sex-ratio occurred.

June 1965

Table 11. Percentage composition of Gammarus population.

June 1965

	June 1		June 16			June 23		
	Repro- ductive	Total	Repro- ductive	Imma- ture	Total	Repro- ductive	Imma- ture	Total
% of ♂	54	54	23	53	23	2	94	2
size range in mm.	13 - 18		14 - 16	2 - 3	53	14 - 16	3 - 4	94
% of ♀	46	46	24		24	4		4
size range in mm.	11 - 14		12 - 14			12 - 13		
Total		100	47	53	100	6	94	100

The samples collected on June 1, contained 54% males and 46% females. Females were all still gravid, with their broods in an advanced stage of development, almost ready to be released, having completed an incubation period of 3 to 4 weeks. No moulting had occurred after ovulation and size class frequencies remained the same for females. Mortality had already ensued in the male section of the population after an active period of precopula, and a slow shift in sex ratio favoring females was noticed.

Between June 5 and June 9, females which started bearing brood early in May, had begun to release immature gammarids, and there was a continuous recruitment of these immatures during the next few weeks. As observed in the field the newborn gammarids measured 2 to 2.5 mm. in body length, included in the 2 mm. size class. Many females died after the release of the first brood.

By June 16, 53% of the total population were found to be the newly recruited immature gammarids and 47% formed the parent population. Nearly half of this parent population were breeding females which had not yet released their brood. The rapid change in population structure became even more evident in the June 23 sample, by which time more females had released brood. The immatures belonging to 3 and 4 mm. classes constituted 94% of the population. Of the 6% adult population nearly $\frac{2}{3}$ were females.

From a closer examination of the females in the parent population, it was found that by June 30, the first reproductive phase was over, and there were no females which had eggs in the brood pouch. Though the adult population was depleted considerably, among the survivors

there were more females than males, (66% ♀ and 34% ♂).

July 1965

Table 12. Percentage composition of Gammarus population

July 1965.

	July 5			July 21		
	Reproductive	Immature	Total	Reproductive	Immature	Total
% of ♂	4	87	4	1	97	1
size range in mm.	14 - 17	2 - 7	87	11 - 16	2 - 8	97
% of ♀	9		9	2		2
size range in mm.	11 - 14					
Total	13	87	100	3	97	100

The few surviving females, which had already released their brood, moulted, and after a short period of precopula, produced a second brood of eggs. Thus on July 5, it was observed that a small section of adult females (about 2% of the total population) had laid eggs into the brood pouch. By this time a certain mortality had occurred among the immature gammarids, and they formed only 87% of the total population, as compared to 94% in June. Further changes occurred in July with the release of the second brood after a much shorter incubation period of about 2 weeks. On July 21, the second set began to appear in the population. By this time the late recruits from the first brood, had grown to 3 to 3.9 mm., whereas the newborns were in the 2 mm. size class. Taking a separate count of

the different size classes, it was found that of the total population, 3% were reproductive adults, 93% were the recruits from the first brood, and only 4% formed the second batch. It was difficult to follow up this second set as the body lengths of the late arrivals from the first brood and early arrivals from the second batch seemed to merge within a short period due to the greater growth in early instars of the second brood. In subsequent estimations these were grouped together as the second set in relation to their age structure. The early recruits from the first brood showed a mean body length of 6.8 mm., the late recruits from the same batch measured 3.5 mm., while the early recruits from the second brood had a mean body length of 2.2 mm.

During the last week in July, with greater addition of immatures into the population the total percentage of the new generation formed 97%. The remaining 3% were reproductive adults. Samples taken on July 31, did not contain any female bearing eggs. Thus breeding and recruitment came to a close by July 31. Including the time when gammarids were in precopula prior to ovulation, the total breeding period extended approximately from the first week of May to the last week of July, a period of 3 months.

The continuous recruitment over this period brought about a rather heterogeneous distribution of age structure in the population as revealed by the size class variation from 2 to 18 mm. On July 31, only two of the life stages constituted the entire population, the post-reproductive adults of the parent population, and the immatures of the new generation.

August 1965

Table 13. Percentage composition of Gammarus population.

August 1965

	August 10				August 25			
	Post-reproductive	Juvenile	Immature	Total	Post-reproductive	Juvenile	Immature	Total
% of ♂	0.4	34	33	34.4	0.5	36	26	36.5
size range in mm.	13 - 16	8 - 10	2 - 6	33	13 - 17	9 - 11	4 - 7	26.0
% of ♀	0.6	32		32	0.5	37		37.5
size range in mm.	11 - 14	7 - 9			12 - 14	7 - 10		
Total	1.0	66	33	100	1.0	73	26	100

By August 10, 99% of the population was composed of juveniles and immatures, and 1% of post-reproductive adults. The secondary sexual characters, calceoli and genital papillae in the male and rudimentary oostegite in the female, began to appear in the first batch of juveniles during the first week of August. Individuals 7 mm. and larger could be distinguished as to their sexes. On August 10, the mean body length of the males was 9.0 mm., and of the females was 7.7 mm. The size classes in the population varied from 2 mm. to 10 mm. The smallest classes of 2 and 3 mm. individuals, the late recruits from the second batch, combined with other immature gammarids which had not yet developed secondary sexual characters formed 33% of the whole population.

These individuals are centered in the figures, below the level of sex-distinction. The absence of any further recruitment was also clear from the sample taken on August 25, when the smallest individuals in the population measured 4 mm. The progressive increase in the size classes of 8, 9, 10, and 11 mm. was also evident.

The sex ratio in the new generation was found to be even. A majority of the males belonged to the 10 and 11 mm. size classes, while females belonged to 8 and 9 mm. size classes.

September 1965

Table 14. Percentage composition of Gammarus population.

September 1965

September 28					
	Post-repro- ductive	Pre-repro- ductive	Juvenile	Immature	Total
% of ♂	1.4	23	14	24	38.4
size range in mm.	13 - 16	11 - 23	9 - 10	5 - 8	24.0
% of ♀	0.6	28	9		37.6
size range	14	10 - 12	9		
Total	2.0	51	23	24	100

The samples taken on September 28 still showed a large number of immature gammarids (24% of the population) where sexes were not distinguishable. Apparently with the seasonal fall in temperatures, the growth rate was slowed down considerably, particularly in the late

recruits of the second batch. Due to the mortality of immatures and juveniles, a slight increase in percentage of the adult parent population was noted, when they formed 2% of the population.

It is interesting to note that in the second batch of juveniles, some had reached body lengths of 7 and 8 mm.; but secondary sexual characters had not yet appeared. Evidently the appearance of these characters was delayed probably due to the prevailing lower temperatures. Thus for the September 28 sample the limit of sex distinction was at the 8 mm. level, compared to the 7 mm. level for August 25 sample and 6 mm. level for August 10 sample (Figs 13 and 14). The mean water temperatures for the two week period prior to these dates were 10.7°C., 19.5°C., and 24.2°C. respectively.

Only 25% of the surviving post-reproductive adults were females, and the rest were males, which showed the greater longevity of the males. The body lengths of these individuals varied from 14 to 16 mm. in males while the females were all in the 14 mm. group. The newly recruited section of the population, well on their way to adulthood, had a mean body length of 11.3 mm. for males and 9.9 mm. for females.

October 1965

Table 15. Percentage composition of Gammarus population.

October 1965

Oct. 22					
	Post-reproductive	Pre-reproductive	Juvenile	Immature	Total
% of ♂	2	32	0	34	34
size range in mm.	14 - 18	11 - 14	-	6 - 8	34
% of ♀	0	30	2		32
size range in mm.	0	10 - 12	9		
Total	2	62	2	34	100

Due to mortality in the various age groups, an increase in the percentage of juveniles below the limit of sex distinction was observed, though they had increased in body length. Post-reproductive adults still constituted 2% of the population. About 62% of the population could now be recognized as pre-reproductive adults. The post-reproductive adults were in the size range 14 to 18 mm. which were mostly males, and the pre-reproductive adults had body lengths from 9 to 14 mm. with an even sex ratio. The immatures had a mean body length of 7.3 mm. and only 2% were in the juvenile range.

November 1965

Table 16. Percentage composition of Gammarus population.

November 1965

November 5					
	Post-reproductive	Pre-reproductive	Juvenile	Immature	Total
% of ♂	2.79	45	3	-	50.79
size range in mm.	14 - 18	11 - 14	10	0	
% of ♀	0.21	30	19	-	49.21
size range in mm.	15	10 - 14	7 - 9	-	
Total	3	75	22		100

The November 5 sample showed 3% of post-reproductive adults and 97% pre-reproductive adults. By this time, all the juveniles noticed in the previous sample had developed the secondary sexual characters. The sex ratio was even and a broader distribution of size classes was evident. The pre-reproductive adults and the sexually distinct juveniles ranged from 7 to 14 mm., while the 3% parent population ranged from 15 to 18 mm. Apparently the males and females had moulted once during the period and moved on into the next higher size classes, which accounted for the increase in the 13 and 14 mm. class of males and the 12 mm. class of females. The lower limit of sex distinction at the 6 mm. level (Fig. 14) confirmed the assumption

that secondary sexual characters could appear in the same 6 mm. class of individuals at lower temperatures after a longer lapse of time. Probably the total metabolism of the individual over a period of time had a greater effect on the expression of these characters than the attainment of a particular size.

December 1965

Table 17. Percentage composition of Gammarus population.

December 1965

Dec. 4					
	Post-reproductive	Pre-reproductive	Juvenile	Immature	Total
% of ♂	0	44	6	-	50
size range in mm.	-	11 - 16	8 - 10	-	-
% of ♀	0	36	14	-	50
size range in mm.	-	10 - 12	7 - 9	-	-
Total		80	20		100

The collections made on December 4, contained only pre-reproductive adults which showed an even sex ratio of 50:50. A partial elimination of the smaller size classes of 7 and 8 mm. individuals was evident from the lower percentages of these. The 12 mm. class of females were also reduced in number. But, the majority of males and females were in the same size classes: 11, 12, 13, and 14 mm. for males and 9, 10, and 11 mm.

for females. Thus, by December a more restricted age distribution was observed in the population, ages competent enough to go through the winter conditions. In the subsequent winter months of January, February, and March 1966, there was cessation of growth and moulting. Mortality affected the lowest and highest size classes, favoring the survival of the potentially more important section of the population with higher breeding capacity.

The description of samples for January, February and March 1966, is given at the beginning of this account, for the sake of comparison with the corresponding samples of the year 1965.

VIII. SEX RATIO

One interesting phenomenon associated with the population dynamics of biparental organisms, is the sex ratio. In most of them the sex is determined at the time of fertilization, one of the sexes being heterogametic, and the initial sex ratio tends to be even. Though we do not yet know which of the sexes in Gammarus lacustris is heterogametic, sexes could be distinguished from the time gammarids were two months old, on the basis of distinct secondary sexual characters already described.

In the present study, the sex ratio of the juvenile gammarids prior to adulthood, was found to be more or less even, 47% males and 53% females in 1964, and 49% males and 51% females in 1965 (Table 18), being the combined ratio for the months of August, September, and October. By the end of October, the juveniles had become mature and formed the pre-reproductive adults of the population, in which stage they overwintered. This was the time when the sex ratio showed great variations from year to year. In 1964-65 winter, the pre-reproductive adults showed a sex ratio of 63% males and 37% females, while in 1965-66 the ratio was 58% males and 42% females for the same period. A general preponderance of males over females during the winter months was clearly evident. This was a period of general mortality in the population due to the prevailing conditions of winter stagnation. The change in the patterns of sex ratio was brought about by inequalities in the mortality of the two sexes. Apparently more males were able to survive the winter months. The slight increase in the percentage of females in 1965-66 winter as compared to 1964-65, may be explained as follows. The mortality experienced by the female population was much greater in 1964-65, when the

Table 18. Gammarus population - sex ratio (%) 1964, 1965 and 1966.

Stage of Life Cycle	Month	1964 - 1965				1965 - 1966			Approximate Age in Months
		Male	Female	Seasonal average		Female	Seasonal average		
				Male	Female		Male	Female	
Juvenile - Pre-reproductive	August	47	53		46	54			2
	Sept.	-	-	47	50	50	49	51	3
	Oct.	-	-		50	50			4
	Nov.	66	34		50	50			5
	Dec.	67	33		60	40			6
	Jan.	63	37	63	67	33	58	42	7
Reproductive - Reproductive	Feb.	56	44		66	34			8
	March	64	36		46	54			9
	May	68	32						11
	June	46	54	50					12
Post-reproductive - Reproductive	July	37	63						13
	August	56	44						14
	Sept.	69	31						15
	Oct.	90	10	77					16
	Nov.	94	6						17
	Dec.	-	-						

onset of winter was rather sudden and many of the smaller size classes, from the second batch, were eliminated before they could reach the pre-reproductive stage of their life. In the 1965-66 winter, though earlier spells of cold weather slowed down the growth rate, more juveniles reached the pre-reproductive stage prior to winter stagnation. Thus a comparatively larger section of the female population was able to survive.

Further shifts in sex-ratio occurred during spring and summer, which was the breeding time. During the breeding period of May, June and July the sex ratio was found to be 50:50. As definitely more males got through the winter months, this equalization in sex ratio signified a greater mortality of the males. This was evident from the reproductive behavior of the two sexes. The males were most active during early spring when they carried about the passive females in precopula, until ovulation and fertilization were accomplished. After the termination of precopula while the females were still carrying the brood, males started dwindling in numbers as a result of natural mortality which followed a period of high metabolic activity. The spring arrival of aquatic birds which fed on gammarids also caused a certain mortality which affected both sections of the population. Though the average sex ratio for the breeding season was even, it must be noted that there were more males at the beginning of the season, whereas towards the close of the season there were more females, as was observed in July 1965, when 63% of the breeding adults were females.

After the release of the brood in July, there was heavy mortality in the female population and the sex ratio once again started shifting in favor of the males. This was the post-reproductive period, August

through December, when the parent adults constituted only 2 to 3% of the whole population, the rest being newly recruited gammarids, less than 6 months old. As seen from the table, among the post-reproductive adults more males were seen to survive from the month of August onwards until by November, almost 94% of these adults were males.

Otto Kinne (1953) observed similar variations in sex ratio in Gammarus duebeni at Keil, leading to the preponderance of males. He considered temperature as the chief controlling factor, and demonstrated experimentally a temperature sensitive phase in oogenesis prior to egg laying. During this phase, if the female parents were exposed to 4.5°C. even for a single day, all the offspring were males. If the father alone was maintained for a fortnight at 4.5°C., and if copulation occurred one or two days after return to 13°C., the offspring were again exclusively male (Charniaux-Cotton, 1960).

Hynes (1954) in his studies on the same species at Gansey beach on the Isle of Man, reported that in most months the males predominated and stated that this was almost certainly due to the smaller undetermined specimens being females though during the months of February, March, April and May when the true ratio could be determined, the female to male ratio was found to be 2.4, 1.5, 1.1, and 0.9 respectively. He also noticed that once breeding started, there was a rapid decline of the female population, and in later samples large males were seen to persist long after the death of the mature females, suggesting thereby that the elimination of the older females from the population might have been due to the lower temperatures. Somewhat in agreement with Kinne, the possibility of a critical temperature affecting the sex ratio was not ruled out, though this critical temperature might have varied with the

temperature to which gammarids were adapted.

In the light of the views expressed above, a few facts have to be reiterated with reference to the field observation made on Gammarus lacustris in Big Island Lake. The peak of reproductive activity leading to precopula, ovulation and fertilization was observed during the month of May 1965, when the mean water temperature for the period was 12°C. The equality of the sex ratio in the new born could be inferred from the observations on sexually distinct juveniles when they were more than 2 months old. Apparently the sex ratio was unaffected by the temperature conditions which were present prior to ovulation. Moreover, the fluctuations in sex ratio occurred only during the pre-reproductive, reproductive, and post-reproductive periods of the adult population, corresponding to winter, summer and autumn seasons. Differential mortality of the sexes was the chief cause of the fluctuations observed. The influence of temperature rather than being direct as in the case of Gammarus duebeni, was indirect in Gammarus lacustris, to the extent that it might have altered the metabolic rates of the individual sexes and their consequent mortality.

Macarthur and Baillie (1929 I and II) in a series of admirable papers discussed fully the effects of metabolic activity on the duration of life, appropriate enough for reference in the present context, because our knowledge of the genetic mechanisms involved in the determination and differentiation of sex in Crustacea is far from satisfactory. In their experiments with Daphnia, they found that the rate of growth, the age at sexual maturity, the size of the brood, the interval between broods and the age at death were all strikingly influenced by temperature and other conditions. As between sexes, the duration of life of males

responded more sensitively to temperature alterations. Within the temperature ranges studied, the Q_{10} for males was about 15% higher than the Q_{10} for females. A rise from 18°C. to 28°C. abbreviated male life far more than it did the female life. Likewise, a drop from 18°C. to 8°C. lengthened the male span far more than the female span. Thus a greater incidence of mortality was experienced by the males at higher temperatures while at lower temperatures, mortality of the females was higher. A close parallel was observed in the Gammarus population, greater mortality of the males in summer, and females in winter. This was in full agreement with the statement expressed by Macarthur and Baillie, "that these results are the expression of the most fundamental sex difference and that they naturally follow from the effects of temperature upon organisms otherwise similar but possessing different initial metabolic rates and susceptibilities." Kinne's findings on Gammarus duebeni indicating that colder conditions favored the production of male offspring, gives further credence to their statement that the same conditions which favored the production of one sex will also favor the survival of the same sex in mortality experiments.

Gammarus lacustris males were found to be generally more active than females, especially during the breeding season. Even during the winter months, they were observed to pursue females actively, and engage in precopula, though the females were not yet ready to bear the brood. This functional difference between sexes accompanied by differences in their metabolic rate has been emphasized by many authors. (Geddes and Thompson, 1899, Riddle 1916, Geiser 1924).

Thus, according to the metabolic theory of duration of life, the males which exhibited greater activity had a shorter duration of life in general. This was found to be the case in Gammarus, where following a high period of activity concerned with precopula, copulation and fertilization, during the breeding season, they started dying off sooner than the females which were still carrying the brood. The greater winter survival of males was thus balanced by their greater summer mortality. The apparently increased percentage of males seen during the post-reproductive period, was evidently due to the large surplus of males observed at the start of the season, and a certain section of this population, not engaged in copulatory activity, could survive for a longer period far beyond their normal duration of life. In contrast, all females had a chance to mate and bear the brood at least once during the season, after which they died. Only a very small fraction of the surviving female population reproduced a second time during the same season.

The later onset of mortality in the female population was clearly indicative of the greater natural longevity of the female, though the presence of a large surplus male population shifted the ratio in their favor towards the close of the breeding season in spite of the already heavy mortality suffered by males. Considering the fact that in Gammarus a single act of fertilization could produce only a single brood, and since each oviposition and fertilization had to be preceded by the precopula, the provision of a larger number of males at the beginning of the reproductive period was distinctly advantageous to the population as a whole by ensuring male partner for every female, and in turn the greater realization of the breeding potential. The reproductive function

in itself was expensive to both sexes, as was shown by the mortality of the males after precopula, and the death of the females after the release of the brood. Regarding the proportionately greater abundance of males in winter months, it might be due to the comparatively higher resistance of the metabolically more active individuals to the deleterious effects of the environment. As stated by Pearl (1922) the males by virtue of their higher metabolic rate were able to acclimate better, but as the external conditions improved both sexes tended to reach their full natural term of life, and the greater natural longevity of females became more evident.

As reported in the present study, there were no set patterns of sex ratio which one could predict. On the contrary, environmental fluctuation had its marked effect.

IX. MORTALITY

The seasonal fluctuations in population density of Gammarus lacustris on either side of the maximum level observed in July were brought about by the mortality experienced by the individuals at different periods in the life of the population. Though the normal duration of life was about 13 months, not all individuals were able to realize this ecological longevity due to various environmental factors, chief among which were temperature and oxygen. The greatest mortality occurred among the immature and juvenile stages, the most vulnerable sections of the population. Natural death by endogenous senescence at the end of the life-term affected the post-reproductive adults of the population, while the pre-reproductive adults suffered most during the winter months.

During 1965, the rapid recruitment of immatures during a short period of two months, June and July, resulted in a sudden increase in the population level. This was soon followed by a quick decline in numbers, as there was not continuous recruitment.

The newborn immature gammarids, though well-equipped for life, could not survive the open waters, at least for the first few days of their life. This was evident from the field collections when these newborn immatures were found only in the cattail regions and the mud shores of the littoral zone. Probably in the open lake, there was always the danger of being floated up in the turbulent waters to be caught in the surface tension. Many were observed to have been trapped in this manner. Such an effect of the surface film of water on the newborn immatures was observed in the laboratory. In the absence of shelter, newly hatched gammarids were seen to be floating in the aquaria. Unless pushed down,

they were unable to sink and many died within an hour.

Thus the open lake was an adverse habitat for the newborn. Within a few days after birth, the immatures were able to withstand the forces of water current and surface tension, and they were found in moderate numbers in the open lake along with the myriads of Daphnia.

Predation by carnivorous insect larvae and nymphs was another factor which contributed to the mortality of immatures and juveniles. Aquatic birds also preyed upon the gammarids in large numbers.

During the peak period of recruitment, density-dependent factors also must have played an important part in increasing the mortality of gammarids. Intraspecific competition, predation, parasitism and disease are all biotic agents which can be called density-dependent (Smith, 1935). Wilder (1940) reported experimental evidence of increased mortality in Hyalella azteca, when cultures were maintained at higher densities beyond a density threshold.

It cannot be stated with certainty at present as to how far the prevailing high temperatures during the month of July affected the survival of the population.

While many factors operated together during the summer months, the winter incidence of mortality, which affected the juveniles and pre-reproductive adults, was primarily due to falling temperatures and severe depletion of oxygen. At the start of winter, there was no shortage of oxygen, but, the rather sudden drop in temperature seemed to affect the smaller age groups.

The heaviest mortality in the pre-reproductive section of the population which was also the overwintering stage, occurred during the month of March 1965. By this time anoxic conditions developed in the lake below the ice, due to prolonged winter stagnation. Large numbers of dead individuals could be seen in the collection for this period. While there was no demonstrable oxygen in the lake water, there was a fairly high content of hydrogen sulphide, over 0.5 ppm. Thus the hazard of overwintering certainly had its decimating effect on the population. During early spring, immediately prior to the onset of reproductive activity, a certain mortality affected the population. This might have been partly due to the rather sudden changes in the ionic composition of water which followed the thawing of ice, and partly due to predation by the newly arrived aquatic birds.

The differential mortality of the two sexes during the pre-reproductive and reproductive stages of adult life has already been referred to in previous section on sex ratio.

This brings us to one interesting aspect, namely the winter survival of gammarids. Though our knowledge about the specific adaptations is limited, a reference may be made to what little is known.

Krog (1954) in his experiments with Gammarus limnaeus from Goose Lake in Alaska, where conditions during winter months were somewhat similar to those reported in the present study, observed a significant lowering of oxygen utilization in these animals at a time when the oxygen content in the lake was lowest. He stated that "Fall of oxygen consumption in response to fall of oxygen content of the lake, rather than elevation

of oxygen consumption in response to lowered temperature of the lake, is regarded as an instance of adaptation to the most critical environmental factor."

This may also be true of gammarids in Big Island Lake, with decreasing levels of oxygen during the winter months. As to their ability to withstand anoxic conditions in the lake nothing is known. Juday (1908) reported that several animals including a mollusc, annelids, and the larvae of several insects, annually passed periods of three to four months at the bottom of Lake Mendota in an environment in which oxygen could not be demonstrated. The views expressed by Cole (1921) in this connection may be cited here. He considered it possible that a process in the decomposition of plant tissues, even under anaerobic conditions, might liberate small amounts of oxidizing substance, probably atomic oxygen, which should be sufficient for their survival. Even in such forms where the presence of a blood pigment has been invoked as a special adaptation to tide over anoxic conditions, he is of opinion, that the amount of oxygen the pigment is able to fix and hold is negligible when compared with the amount necessary to liberate the energy expended during the total time when the dissolved oxygen is lacking in the surrounding water.

Such speculations are challenging enough for detailed investigations on survival under anoxic conditions, and Gammarus lacustris population in Big Island Lake should prove an excellent subject.

X. LONGEVITY

The ecological longevity, or the observed life duration of gammarids in the population was found to be about 13 months. A small section of the population lived as post-reproductive adults for a further period of two to three months, after which, only a negligible fraction continued to live beyond their normal span of life. Such individuals reached a maximum age of two years, which should be considered as the longest possible longevity, a fair approximation of their physiological age or the duration of life under optimum conditions.

According to Bodenheimer (1958), the life-span of an organism can be divided into three ecological ages, (a) development, lasting from fertilization of the egg until first birth, (b) the reproductive period, lasting throughout reproduction, and (c) the post-reproductive period of senescence.

The relative durations of these three types of ecological ages in G. lacustris were calculated on the basis of the life-cycle of an average individual which reproduced only once, and lived for a total period of 395 days, (Table 19, Fig. 15).

The development period alone constituted 88.6%, as it included the incubation period, immature and juvenile period and the pre-reproductive period during which the gammarids overwintered. As stated by Bodenheimer (1958), similar condition is observed in short-lived insects like the Ephemeridae where there is a shift of the total feeding period into the larval state. But, in Gammarus, the extended pre-reproductive period necessitated by the winter conditions is the main cause.

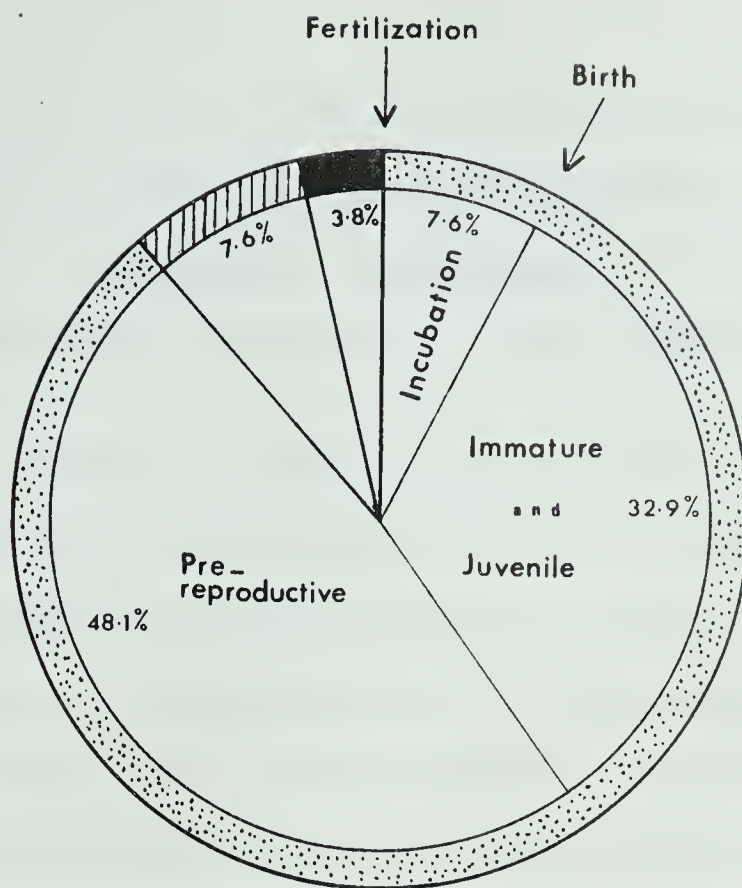
It must be emphasized, however, that these ecological ages for a particular species will be governed by the particular combinations of environmental factors, and no generalizations are possible. In contrast to other species of Gammarus, G. lacustris, is seen to have an unusually short breeding period, as has been already inferred by Hynes (1955) for the same species from Northern Europe, where summers are short, and stated that "such a life-cycle would appear to be admirably adapted to such conditions."

Table 19. Relative duration of ecological ages
in Gammarus lacustris.

Total duration of life in days	Ecological age	Duration in days	% of total life duration
395	I Developmental		
	a) Incubation	30	7.6
	b) Immature & Juvenile	130	32.9 88.6
	c) Pre-reproductive	190	48.1
	II Reproductive	30	7.6
	III Post-reproductive	15	3.8

Figure 15. A modified pie diagram showing the relative percentage duration of the three ecological ages in Gammarus lacustris. (Based on Table 19).

FIG. 15



	Developmental	88.6%
	Reproductive	7.6%
	Post-reproductive	3.8%

XI. EPIBIONTS AND PARASITES

Epibionts

The long intermoult periods of pre-reproductive and reproductive adults were found to be successfully utilized by many stalked ciliates such as the Vorticella sp., Epistylis sp., Zoothamnium sp. and Carchesium sp., which lived as epibionts, attached to the body surface of gammarids.

Mohr (1952) reported the occurrence of a sessile ciliate of the order Chonotricha, on the overwintering adults of G. setosus, and considered it as an adaptation of this particular ciliate, which lacks any resistant stages, to overcome the winter by attaching itself to the comparatively more active crustacean host. Meshkova (1958) reported ten species of individual and colonial, suctorial and ciliate Infusoria distributed on various body regions of G. lacustris found in Lake Sevan in U. S. S. R., and observed that when the host crustacean moulted, the Infusoria left their sites for a new host. Similar shifts could be inferred from the absence of epibionts on newly moulted gammarids in Big Island Lake. Though generally these epibionts were not at all harmful to the host, occasionally some individuals were found to be immobilized by an unusual bloom of attached filamentous fungi, in combination with the stalked ciliates on the body surface.

Parasites

In the course of routine examination of gammarids in the laboratory, occasional observations were made on some of the parasites found in them. Though no detailed study was attempted, it was possible to estimate the percentage of infected individuals in the population.

The chief parasites found were the encysted cystacanths of acanthocephalans and cysticerci of cestodes. The cystacanths were generally colored yellow or orange and could be easily noticed through the somewhat transparent integument, while the cysticerci, pale white in color, could be observed only after squeezing out the contents of the body cavity. Very often multiple infections were observed where the same individual carried more than one cyst of the same parasite and a small percentage of individuals showed both cystacanths and cysticerci.

Out of a total of 600 gammarids examined during the winter months of 1964-65, 13% were found to harbor acanthocephalan cysts. No counts of cestode cysts were made during this period. In the spring and summer of 1965, counts of both cystacanths and cysticerci were taken. For the months of May and June, a total of 300 breeding adults was examined and it was found that 35% of the population had cystacanths, while 17% had cysticerci. Eight per cent of the population had both cysticercus and cystacanth in the same individual. Two hundred juveniles were examined in August 1965, and a much higher percentage of infection was noticed. Sixty-eight per cent had cystacanths, 24% had cysticerci and 8% had both types of cysts. Thus it was evident that spring and summer were the periods of heavy infestation, when the newly recruited section of the population would have fed on detritus already contaminated with the droppings of aquatic birds, which contained eggs of acanthocephalans and cestodes. The continued prevalence of cystacanths and cysticerci in overwintering pre-reproductive adults, though in lesser numbers, was indicative of the survival adaptation of the parasite as well, until the arrival of the final host in the following spring and

summer. While the cystacanths and cysticerci were found encysted within the haemocoel, another parasite which was most common in the alimentary tract of gammarids was a gregarine, which fully agreed with the description of the polycystid gregarine Rotundula gammari from Gammarus pulex, first reported by Pixell Goodrich (1949).

Amphipods in general have been reported to be well established intermediate hosts for trematodes, cestodes, and acanthocephalans. Hall (1929) De Giusti (1949), Belapolskaya (1957), Hynes and Nicholas (1957), Kovalenko (1961) Awachie (1963), and Schmidt (1964) and others have referred to many species of Gammarus and Hyallela azteca as vectors of these parasites. From Alberta, Connell and Corner (1957) reported a higher extensity of infection and found 28 out of 62 amphipods from Elk Island Lake infected, which had 1 to 3 cysts per individual.

Garkavi (1956) reported the natural localization of streptocariasis in ducks found in lakes of Western Siberia, through the abundance of G. lacustris, which is the immediate host of the parasite Streptocara and mentioned that new foci of streptocariasis were always associated with the dispersal of gammarids by birds.

Hynes (1955) in his studies on G. lacustris from Wales, observed about 30% of the population infected with the acanthocephalan Polymorphus minutus, and in agreement with the earlier findings of Le Roux (1933), stated that the infection interfered seriously with breeding and sometimes prevented it altogether by causing sterility in the female.

In order to find if a similar situation existed in the gammarid population of Big Island Lake, several females were examined during the

breeding season. No reduction in fecundity was observed as a result of the acanthocephalan parasite. Though many brood bearing females were found to be infected, there was neither a significant difference in the mean number of eggs per female, nor any adverse effect on the development of brood within the brood pouch, as the stages were all comparable to the ones observed in uninfected individuals. However, in the case of individuals infected with cestodes, some females had a higher intensity of infection showing 5 to 20 cysticerci in the same individual. Such specimens were rather stunted and the embryos within the brood pouch had an irregular and deformed appearance which probably indicated an arrest of development. Such individuals were too few to be of any consequence to the population as a whole.

Specific identification of the parasites was not possible. The most common acanthocephalan species reported by Gallimore (1964) from the aquatic birds of Big Island Lake was Polymorphus paradoxus. It was therefore presumed that the intermediate stage of this parasite was more abundant in the gammarid population of the same lake, which constituted a major food item for these birds. In a local study, Erwin Heubner (1965) was able to recover adults of Polymorphus paradoxus (?) by suitable feeding experiments using gammarids from the same population.

From the data at hand, it can only be stated rather presumptuously that cystacanth infection caused no perceptible interference in the normal life cycle of G. lacustris in Big Island Lake probably because these are already well-established intermediate hosts.

Hynes (1955) gave a plausible explanation for the unaccountable disappearance of G. lacustris in West Southerland reported by Reid (1951) on the basis of heavy infestation of such populations with Polymorphus minutus.

Considering the variety of parasites found in G. lacustris nothing can be said definitely as to which of these is more harmful to the host until proper identification of these parasites is carried out. Interesting results are awaited from the work now being carried out by Michael Denney at the University of Alberta, on these parasites found in Gammarus lacustris.

XII. DISCUSSION

The amphipod community in Big Island Lake was found to be dominated by Gammarus lacustris along with one other member, Hyalella azteca, which was found in moderate abundance. The present discussion is in relation to G. lacustris population, observed over a period of two years which covered one complete life cycle. Though the main focus of study was on the relative abundance with respect to habitats, it was also possible to have a general idea about the population dynamics of the species. Considering the non-random distribution of gammarids in the lake, each specified habitat was sampled separately, and the relative abundance was expressed empirically as the number of individuals per 100 liter volume of water. By pooling the data for each specified month and habitat, the total abundance was also estimated with respect to the lake environment as a whole. Compared to Hyalella azteca, which was confined to the cattail and Potamogeton areas, and the muddy bottom of the shallow lake, the greater swimming ability of gammarids enabled them to exploit the open waters as well. This certainly provided ample dispersion, and to a small extent, must have ameliorated the pressures of competition, particularly where overlap of niches occurred. Very seldom did Hyalella appear in the open lake samples.

Odum (1953) stated that species which have similar morphological and physiological characteristics may have the same niche requirements. But competition occurs whenever niches overlap even to a partial extent. Andrewartha and Birch (1954) also referred to competition as the relationship between species which utilize the same food and space.

The consistently higher numbers of gammarids observed in all habitats

showed that Gammarus was the more successful of the two.

Hutchinson (1959) observed that "For the larger of two species always to be larger, it must never breed later than the smaller one." This was very true of the gammarid population where there was an earlier onset of reproduction (May and June 1965). In Hyalabella the breeding started a month later. Whereas the new born immatures of gammarids appeared during the first week of June, Hyalabella immatures were not observed until the first week of July. By this time the gammarids had completed the release of the first brood, and most of the new born gammarids had partially moved out into the open lake, from their sheltered habitats.

Thus the earlier onset of reproduction in Gammarus must be considered as an adaptation to overcome severe competition, which would have otherwise been necessary if both had released their young at the same time.

As to the smaller numbers of Hyalabella in the amphipod community, it still remains to be found out whether it was actually due to a shortage of some essential resource or to direct interference from Gammarus.

One of the attributes which has contributed much to the success of gammarids is their wide flexibility in feeding habits. Reports by previous workers, have shown the diverse food items on which gammarids can thrive. Hynes (1954) has reviewed in detail the food habits of gammarids.

Haempel (1908) in Germany analyzed the gut contents of Gammarus pulex and found mostly plant remains, green algae, worms and insects were only occasionally present. Wundsch (1922) in Germany and Mottram (1934) in England, found that the same species preferred dead leaves to most other foods. Margalef (1948b) in Spain, found that the species fed exclusively

on animals, chiefly insects and Cyclops. Clemens (1950) and Hynes (1955) maintained stocks of gammarids on dead elm leaves supplementing it with some animal food. Newly hatched daphnids were also used by Clemens (1950) to feed adults of G. fasciatus, in addition to dog food. Dunn (1954) stated that gammarids are essentially detritus feeders.

Ermolaeva (1962) in U. S. S. R. found in G. lacustris that apart from the remains of plants and animals, the intestines revealed many algae. The intestinal analysis showed the predominance of Protococcales and Diatomaceae, which were not as numerous in the plankton as the Cyanophyceae, and suggested that gammarids showed preference for definite groups of algae.

Though detailed analysis of the gut contents was not attempted in the present study, a few observations made, clearly showed that along with organic detritus, green algae and diatoms were most frequently present.

During the winter months, a few gammarids were observed to feed on chironomid larvae. Pacaud (1942) also observed G. pulex attacking pupae of Simulium. Cannibalism has also been reported (Sexton, 1924).

Probably this euryphagous nature of gammarids is of great adaptive significance in that they are able to overcome the seasonal fluctuation in food supply, by utilizing whatever food is available.

The importance of the habitat in determining the total abundance of Gammarus in the lake has already been described. The most preferred cattail habitat was found to be suitable for all stages of life and was available throughout the six-month period when the lake was free of ice. Thus the extent of the cattail area can be regarded as a limiting factor

in population density of G. lacustris.

According to Thompson (1939) "the discontinuity and variability in habitats, produced by the physical factors, both in time and in space, is undoubtedly the primary extrinsic factor of natural control." The same idea is expressed by Errington (1945) with respect to bird populations, that the characteristic level of abundance is determined primarily by the amount of "cover" in the area, which he called the carrying capacity of the area.

Population dynamics

Dice (1952) stated that "The population of any species in existence at a given time and place depends upon (1) the rate of reproduction of the species and (2) its rate of mortality. When reproduction exceeds mortality, the species will increase in abundance. When on the contrary, mortality exceeds reproduction, the population density will decrease." The balanced situations that we find in nature, where a species is able to maintain optimum levels of population density, or equilibrium density, is itself a dynamic one, depending upon reproduction, rate of recruitment, and mortality.

The rate of recruitment in a population is governed by the number of breeding females, and their age-specific fertility, or the number of living young produced by each female.

A fair estimate of the rate of reproduction in G. lacustris is possible. Since each female is potentially capable of bearing two broods, producing an estimated total of 60 to 70 young, the maximum number a single female can produce over a period of one year will not exceed 70. But the number could be much less, because, many females die off after the

release of the first brood. As compared to other gammarids, G. lacustris at Big Island Lake showed a comparatively low rate of recruitment.

Embody's (1912) studies on G. fasciatus at Ithaca, N. Y., showed that the reproductive season extended over a period of seven months and the average number of eggs laid at a time was 22. Egg laying was repeated on an average of 11 days and he calculated a possible progeny of 24,221 coming from a single pair.

Blegvad (1922) in Denmark found in G. pulex, fourteen to fifteen broods in one breeding season from February to October. Heinze (1932) reported six to nine broods for G. pulex, while Clemens (1950) estimated five to eleven broods for G. fasciatus. Clemens also noted that the breeding and immature populations were both present during the breeding season, approximately half the population being in the breeding stage. This is in contrast to the condition observed at Big Island Lake where at the start of the breeding season (May 1965) only breeding adults were present in the population.

Hynes (1955) stated that G. lacustris (in Wales) produced 100 offspring or less, bearing 3 or 4 broods for the season showing an average of 22 eggs per brood. Death following the final brood was also observed in the adult population. The estimated potential number of offspring from a single pair of G. fasciatus (in England) was 1500 (Hynes 1955).

As compared to these gammarids reported from different geographical areas, where the climatic conditions must have differed, the rate of reproduction in G. lacustris at Big Island Lake, is considerably lower.

This may partly be due to the short summer reproductive period, and consequent limitation in the number of broods a female can bear before the onset of winter.

With reference to starlings, Lack (1948) stated that "The size and kind of reproductive units produced by any species are adaptive characters which must be adjusted to the conditions of existence of the younger animals. Natural selection tends to establish as an inherited character, the rate of reproduction, which is most favorable to the continuing success of each species." Further, "as a specific adaptation for survival, wasteful reproduction is avoided."

Dunbar (1960) also observed that "Frugality in reproduction, is said to be characteristic of highly evolved stable populations which have in the past been subjected to the stress of oscillation in an oscillating system, and that they have responded to selection for this self-regulating character of a restricted breeding rate, tending towards stability."

However, in the gammarid population of Big Island Lake, a slight compensation is apparent in the increased number of eggs per brood, as compared to other gammarids. The number of eggs produced by G. lacustris varied from 30 to 40 in a single brood. The average clutch sizes reported by Hynes (1955) for other gammarids are 19 for G. duebeni, 29 for G. fasciatus, and 16 for G. pulex, all from England.

The increased number of eggs per brood may be due to the prolonged overwintering stage of the pre-reproductive adults. Halfway through the winter, if the pre-reproductive adults are made to breed under laboratory conditions at the room temperature of 17 to 20°C., the number of eggs

per brood varied from 10 to 15. However, it cannot be stated definitely whether the age of the individual or the duration of exposure to the cold conditions is more important in determining the size of the brood.

The fluctuations in the population density of G. lacustris, for the six-month period May to October 1965 are graphically represented in Figure 16. Being an annual life cycle a repetition of the pattern can be expected, with peaks of abundance occurring at intervals of one year.

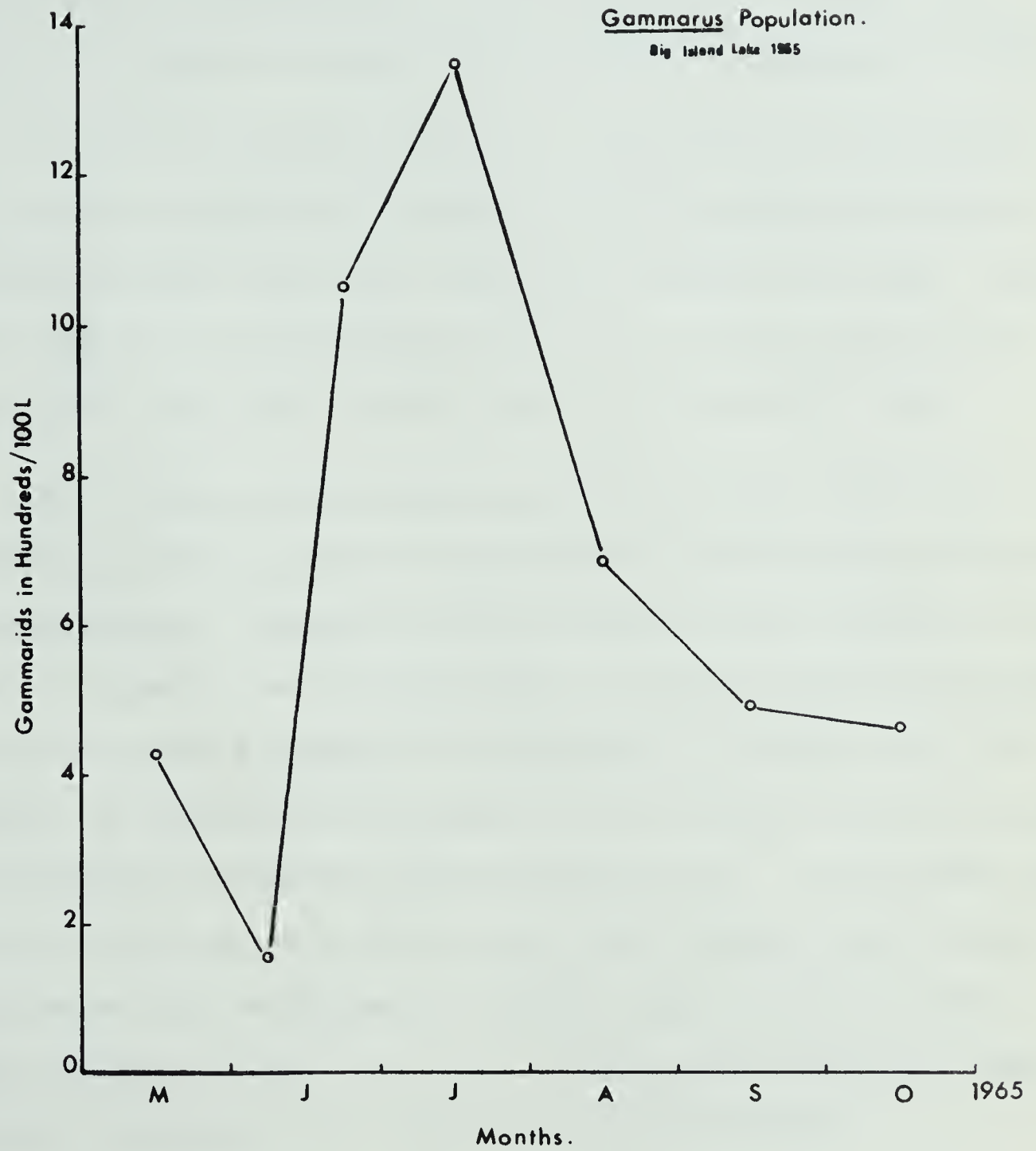
The lowest level of population density, 150 gammarids/100 liters was observed during the first half of June, which was also the breeding period. In contrast the density figure for the month of May was 427 gammarids/100 liters which should more or less correspond to the winter level of the population. This fall in population density during the short period of one month was primarily due to predation by the newly arrived aquatic birds and also due to the greater mortality experienced by the male section of the population after an active period of precopula.

During the second half of June there was a rapid increase in population density, and the peak was reached in the month of July, with 1353 gammarids/100 liters. Thus there was almost a ninefold increase in the population density. By this time about 95% of the population was composed of the newly recruited immature gammarids. This was also partly due to adult mortality of the parent population, after the release of the first brood.

The increasing phase of the population density came to a close in July, and the downward slope of the curve showed the decreasing phase, which was equally steep. Heavy mortality of the newly recruited immatures,

Figure 16. Population growth curve of Gammarus lacustris, Big Island Lake. May to October 1965.
(Based on Table 1)

FIG. 16



brought down the density level to 683 gammarids/100 liters observed in August, only about half of the peak level. From August onwards, the decline was rather slow. By this time the juveniles constituted the major section of the population. Prior to the onset of winter, in October, the population density was found to be 467 gammarids/100 liters.

Estimation of abundance during the winter months was not possible. But a certain mortality was observed during this period, particularly in the month of March, when anoxic conditions prevailed in the lake. However, a major section of the pre-reproductive adults survived till the next spring, when they began to breed, repeating the annual life cycle.

The increasing and decreasing phases of population density coincided in time with the external conditions which may be broadly referred to as the climate. Nicholson (1954) has observed that "climate in itself does not determine the population levels, but permits population increase or causes decrease according to its favorability or otherwise, by its influence on some governing mechanism in the environment" which he called the "legislative" influence of the climatic factors. He also stated that "periodic environmental influences, such as the seasons, tend to impose their period upon oscillations of internal origin, and so to obscure their existence in spite of the fact that they may be dominantly responsible for the violence of the population changes observed."

As stated by Andrewartha and Birch (1954) for insects, it may also be true of gammarids that "a population made up entirely of adults in the reproductive stage, being quite untrammelled by limited space, would at first increase much more rapidly than a population with a stable age

distribution, which would include a high proportion of immature stages."

In G. lacustris, the over-wintering pre-reproductive adult population had a limited age distribution, the maximum age-difference between individuals being only 2 months. This should be considered as the "intrinsic stationary population." Vajdas (1947) observed that a population subject to mortality dependent on age and which is supplied with entrants each year so as to keep the total population constant, tends in general to a limiting age-distribution, "the intrinsic stationary population."

The particular growth form of a population is the product of the interactions between natality, mortality and dispersion. Fluctuation is the rule rather than the exception, as far as population growth form is concerned. The magnitude of the variation can be great or small in terms of the total population size, in terms of the time intervals between fluctuations and in terms of the species involved. For aquatic populations, the physical and chemical qualities of the water, water movements, light penetration, substratum effects and selected aspects of food supply constitute the "density-independent factors."

The individual growth, rate of oxygen consumption, protection from noxious agents in the environment, are considered as "density-dependent", these being the processes affected by the three primary variables natality, mortality and dispersion.

As to the compensatory reaction to external forces, Nicholson (1954) stated that "The persistence of populations in their ever-changing environments, and their maintenance of degrees of abundance, in general conformity with the changing conditions, are wholly dependent upon compensatory

reaction to external forces." "Populations limit themselves by progressively reducing the favorability of the environment as they grow, so maintaining themselves in a condition of balance with their environments, that on the average the number of births equals the number of deaths, imposed destruction not increasing mortality but merely causing a redistribution of mortality amongst the lethal factors, and that compensatory reaction enables them to accomodate themselves to even very severe environmental stresses."

These compensatory adjustments are evident in the Gammarus population. The stages of life cycle that are usually present during the summer, the immatures and juveniles, are not "cold-hardy", whereas the pre-reproductive adults are, and they constitute the over-wintering population. Apparently the pre-reproductive adults have greater capacity for getting acclimatized to the prevailing temperatures, which is a very useful adaptation for animals living in lakes in a temperate climate as has been shown for bullhead, Ictalurus (Ameiurus), by Brett (1944).

The mortality as seen in the gammarid population, though greatest in the newly recruited immature section of the population, was also found, to occur at other stages of the life cycle. The brief agents of mortality were predatory, lack of oxygen, and sudden fluctuations in temperature.

"It has been pointed out by Errington (1956) that the population consequences of specific mortality seldom carry through long enough to affect appreciably the (muskrat) population as a whole. Instead of each agent of mortality depressing the end product in proportion to the numbers of animals it kills, there is a lot of nullification of what are regarded as limiting factors. Not only is there a natural substitution

of one factor for another, but the mortality itself may precipitate responses in the population that tends to offset it." (Krumholz 1963).

Populations such as that of G. lacustris, (where the mortality is highest in the early stages of life), have become adjusted to that type of "natural" mortality, and since such losses are regular, no increase in reproductive activity is necessary, and the current reproductive rate can be considered "normal".

Further studies are needed to discuss the predator-prey interaction, considering importance of Gammarus as a major food item for aquatic birds, which are annual visitors to the lake. Similarly host-parasite relations have also to be fully understood before we can assess the magnitude of such interaction as G. lacustris is found to harbor a variety of parasites, chiefly acanthocephalans and cestodes.

Summary

Gammarus lacustris Sars is a fresh water amphipod, which has a wide distribution in Canada. It is not only an important source of food for fishes and aquatic birds, but also an intermediate host for many parasites, chiefly acanthocephalans and cestodes.

Some ecological aspects of the G. lacustris population in Big Island Lake, Alberta, were investigated with reference to habitat preference, relative abundance, life cycle, age, growth, size and sex ratio over a period of two years, 1964-1966.

Big Island Lake is shallow and eutrophic. The mean water temperatures for the summer months in 1965 varied from 12°C. in May to 22°C. in July. In winter the lake was fully ice-covered and the water temperature was 2°C to 1°C. The percentage saturation of oxygen for the same period was 90% in May, 77% in July and 100% in October. Towards the peak of winter stagnation, in March, there was no measurable oxygen in the lake, whereas 0.5 ppm of H₂S was present. The mean pH values for the months of May, June and July were 8.3, 8.5 and 8.3, while during the winter months it was 7.0.

The overwintering gammarids preferred the mud bottom when shelter in the form of aquatic vegetation was minimal, while in summer they chose specific habitats, mainly along the littoral zone.

Considering their non-random distribution, suitable methods were adopted during the summer of 1965, to determine quantitatively their relative abundance with respect to preferred habitats within the lake. Greater concentration was observed along the shallow shores with emergent

cattail and submerged pondweed vegetation. In the open lake gammarids were in smaller numbers; but they showed a marked preference for the bottom layer as compared to surface and middle layers. A diel variation in horizontal distribution of the population was also observed in the open lake when samples were taken at intervals of 2 hours, during a 24 hour study (July 21 - August 1, 1965).

Sexes are easily distinguishable in G. lacustris on the basis of secondary sexual characters, calceoli and genital papillae in the male and the presence of oostegites and absence of calceoli in the female. These structures first appear as rudiments in two-month-old juveniles. In body length adult males are larger than females by about 2 mm.

In the adult female, the moult immediately prior to ovulation is marked by the appearance of long bristles on the 4 pairs of oostegites which together form a ventral brood pouch.

Soon after the ice-thaw in early spring, the breeding season commences with the pairing of the two sexes (precopula). Ovulation is followed by copulation and fertilization. Along with the water current produced by the pleopods, the sperms are transferred from the genital papillae of the male into the brood pouch of the female, the first pair of pleopods in male helping in the process.

In Big Island Lake most females have only a single brood. The clutch size increases with the body length of female. A majority of females die after the release of the first brood while a few surviving females reproduce a second time.

The incubation period varies in inverse relation to seasonal temperatures. During 1965, the early brood of May and June took three to four weeks for incubation when the mean water temperature for the period was $14.9^{\circ}\text{C}.$, while the second brood in July of the same year took only two weeks, when the temperature was $22.0^{\circ}\text{C}.$

The initial release of immatures began during the first week of June in 1965. New born immatures measured 2.0 to 2.5 mm. in body length. Growth was rapid during the early instars. Within two months the immatures became juveniles (7-10 mm.) when sexes could be distinguished. By the fifth month they became pre-reproductive adults (10-14 mm.) at which stage they overwintered without further growth.

Seasonal fluctuations in sex ratio were evident. While during summer months both reproductive adults and juveniles showed equality in sex ratio, during winter months there was a preponderance of males. A similar shift in favor of the males was also observed among the post-reproductive adults.

In the gammarid population highest mortality is seen to occur among new born immatures. The open lake is an adverse habitat for the new born, as many are trapped on the surface film of water. Predation by aquatic birds, carnivorous insect larvae and nymphs causes mortality affecting all stages of life, while natural death due to endogenous senescence occurs among the post-reproductive adults.

The approximate percentage duration of the three ecological ages are (i) developmental = 88.6%; (ii) reproductive = 7.6% and (iii) post-reproductive = 3.8%, taking the average span of life as 13 months.

A brief account of epibionts and parasites associated with G. lacustris is given.

In relation to total abundance, low numbers were observed in the early spring of 1965, when the gammarid population showed a restricted age distribution mainly composed of reproductive adults. With the rapid recruitment of the new generation, the population level rose to a peak in July, followed by an equally rapid decline due to early mortality of immatures. By the end of August, the population was almost half of the peak level. Further mortality affected the population during winter months, especially in March, when anoxic conditions prevailed in the lake. The surviving pre-reproductive adults carried on the seasonal population cycle with the advent of spring.

A few observations have also been made on the ecological adaptations which have enabled this species to be a very successful member of the lake community.

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Appendix I

Physical characteristics of the water samples - 1965-1966

Date of sample	Air temp. °C.	Water temp. °C.	pH	Oxygen cc./l.	Secchi disc cm.
May 12/1965	-	15.2	8.8	6.0	38
May 15	10.0	11.3	8.0	5.3	38
May 18	10.0	9.3	8.0	-	26
May 21	-	12.4	8.4	7.0	-
June 4	16.5	15.0	8.8	6.0	-
June 7	12.0	16.0	8.6	6.0	-
June 9	28.0	20.0	-	-	-
June 14	21.0	18.0	8.6	5.5	-
June 23	21.0	15.5	8.8	7.3	38
June 30	20.0	17.0	7.6	-	-
July 5	25.0	24.0	9.0	5.0	96
July 12	20.0	19.0	8.2	4.0	49
July 15	24.0	21.0	7.0	3.5	96
July 21	23.0	22.0	8.4	4.8	84
July 27	27.0	24.0	8.9	4.1	52
August 3	29.0	25.9	9.0	6.5	49
August 5	21.0	24.0	9.0	5.0	31
August 10	19.5	23.0	9.8	5.4	26
August 18	24.5	20.5	9.6	5.7	29
August 21	16.0	18.5	9.4	4.5	21
August 25	18.0	19.5	9.6	5.5	21
Sept. 1	13.0	11.5	9.0	7.2	-
Sept. 11	7.0	10.0	9.2	6.4	26
Sept. 28	7.0	14.5	-	7.0	26
Oct. 2	13.0	7.0	9.5	7.0	23
Oct. 22	11.5	6.0	8.0	8.4	31
Nov. 5	0.2	1.2	8.0	5.2	-
Dec. 4	-2	2.0	8.2	4.5	-
Dec. 17	-4	1.0	7.8	1.8	-
Jan. 11/1966	-	1.0	8.6	1.2	-
Feb. 10	-	1.0	7.8	1.0	-
March 10	-	1.0	7.0	0.0	-

Appendix I (cont'd)

Chemical characteristics of the water samples,
1965, expressed in parts per million.

Date of Sample	Total Solids	Ignition Loss	Hardness	Alkal- inity	SO ₄	PO ₄	Ca	Mg
Jan. 16	936	360	15	350	-	-	-	-
Mar. 30	1344	352	787	640	357	-	-	-
May 4	538	176	135	90	171	-	-	-
May 15	422	58	220	150	158	-	-	-
June 1	424	50	200	140	167	2.2	54.4	19.0
June 14	414	146	200	175	93	1.6	59.2	10.2
June 23	424	182	200	185	188	2.2	52.8	16.5
July 5	390	170	165	125	85	0.3	44.8	12.9
July 12	342	158	190	125	64	1.3	45.2	18.7
July 21	352	174	170	160	45	3.8	46.0	13.4
July 27	362	214	260	150	36	2.5	44.0	36.4
Aug. 3	226	122	160	150	11	1.8	47.6	10.0
Aug. 11	348	166	175	175	47	2.9	51.2	11.4
Aug. 18	354	164	240	120	69	2.8	51.3	29.7
Aug. 25	356	170	175	140	61	4.0	50.0	12.1
Sept. 1	382	144	175	180	67	3.2	48.0	13.4
Sept. 17	358	182	195	150	52	2.6	50.0	17.0
Sept. 28	366	194	165	155	44	1.6	46.8	11.6
Oct. 22	360	176	165	135	61	0.9	48.8	10.4
Nov. 5	290	178	210	160	13	0.5	60.0	14.5
Dec. 4	426	220	275	185	54	0.4	56.0	32.8
Dec. 17	462	252	230	200	55	1.7	60.0	19.2

Appendix II

Details of samples against each collection date.

(Generally collections were made between 9 AM and 12 Noon)

Date of Sampling in 1965	Total Catch	No. of gammarids/100 liters of sample						
		Open Lake			Cattail	Mud Shore	Sandy Shore	<u>Potamogeton</u>
		Surface	Middle	Bottom				
May 18	270	2.2	33.6	31.5	----	----	----	----
May 21	1059	5.6	40.5	29.6	900	----	0	----
May 26	424	----	----	----	296	1060	56	----
June 1	707	5.5	22.0	18.2	120	270	115	----
June 4	250	0.2	3.6	6.9	120	----	240	----
June 7	486	1.0	16.0	28.0	450	190	170	----
June 9	530	2.9	15.5	18.1	212	-----	20	----
June 14	815	0.6	9.6	17.8	936	----	620	----
June 23	1988	3.0	21.9	21.4	2616	----	2156	----
July 5	2278	13.4	31.6	46.9	2956	----	2880*	----
July 12	1757	26.1	27.0	39.9	1800	----	----	----
July 15	3332	19.5	61.6	75.9	555	----	3535*	----
July 21	4732	33.7	40.4	52.5	----	----	3535*	1070.0
July 27	2755	5.4	12.4	51.7	720	----	-----	253.7
Aug. 10	2240	12.3	30.0	32.9	1860	----	----	241.0
Aug. 18	1867	11.5	17.7	57.4	3180	----	----	63.6
Aug. 21	3086	40.1	35.5	34.0	490	----	----	502.7
Aug. 25	3123	31.2	19.9	29.2	1463	----	----	286.5
Sept. 1	2910	11.5	8.5	16.9	2080	----	----	376.5
Sept. 17	1875	4.8	25.5	30.2	1050	----	----	260.5
Sept. 28	550	0.4	5.9	17.7	570	----	----	51.0
Oct. 2	3082	15.4	40.1	34.8	1682	----	----	441.3
Oct. 22	1463	4.5	8.0	8.5	250	----	----	395.0

* Flooded shore

Appendix III

A two-factor analysis of variance to determine the habitat preference of Gammarus. Big Island Lake. Gammarids/100 liters of sample. May through October, 1965.

Month	Habitat			Cattail
	Open Lake			
	Surface	Middle	Bottom	
May	2.25	33.6	31.5	900
	5.65	40.55	29.66	296
June	5.50	23.07	18.25	120
	1.0	16.0	28.0	450
	3.0	21.9	21.4	2616
July	13.41	31.60	46.9	2956
	19.5	61.68	73.93	555
	5.41	12.4	51.75	720
August	12.32	30.00	32.9	1860
	11.5	17.75	57.4	3180
	31.2	19.90	29.2	1463
September	11.5	8.5	16.9	2080
	4.82	25.57	30.25	1050
	0.41	5.9	17.7	570
October	15.4	40.15	34.82	1682
	4.5	8.0	8.57	250

Calculations were done following the steps given in Simpson, Roe and Lewontin (1960, pages 280-285) and the results are entered below.

Source	Sum of Squares	Degrees of Freedom	Mean Square	F
Months	714120.93	5	142824.18	0.56
Habitats	16467480.90	3	5489160.30	21.67
Interactions	5108297.13	15	340553.14	1.34
Deviations	12153137.75	48	253190.36	

A two-tailed t-test for the significance of the difference between the means of population density in cattail and Potamogeton habitats (July 21 to Oct. 22, 1965)

gammarids/100 liters.

Date	Cattail	<u>Potamogeton</u>
July 21	---	1070
July 27	720	254
August 10	1860	241
August 18	3180	64
August 21	490	503
August 25	1463	286
September 1	2080	376
September 17	1050	260
September 28	570	51
October 2	1682	441
October 22	250	395
Total	13345	3941

Following the procedure given in Simpson, Roe and Lewontin (1960, page 176) a t value of 11.41 was obtained.

Appendix IV

A two-factor analysis of variance to determine any significant difference in the vertical distribution of gammarids between the months of May through October 1965. (Method same as followed in Appendix III.)

No. of gammarids/400 liters

Date of Sampling	Open Lake		
	Surface	Middle	Bottom
May 21	9	158	164
	37	90	76
	22	117	116
June 23	8	52	36
	24	96	93
	4	115	128
July 21	154	84	110
	93	223	329
	158	178	192
August 25	123	55	87
	176	98	104
	76	86	160
September 28	0	8	35
	4	34	95
	1	29	83
October 22	10	21	30
	16	37	28
	28	38	45

Source	Sum of Squares	Degree of Freedom	Mean Square	F
Months	126294.93	5	25258.98	14.60
Layers	26340.76	2	12170.38	7.61
Interactions	44108.79	10	4410.87	2.54
Deviations	62281.34	36	1730.03	

Appendix V

A single factor analysis of variance to determine as to which of the three layers in the open lake is most preferred by gammarids. (Only samples collected in July 1965 are considered.)

Gammarids/400 liters

Date of Sampling	Surface	Middle	Bottom
July 5	47	82	69
	75	180	102
	38	118	392
July 12	79	95	123
	53	137	128
	182	192	228
July 15	84	269	300
	35	262	479
	91	295	338
	102	161	98
July 21	154	84	110
	93	223	329
	158	178	192
July 27	17	38	120
	25	51	306
	23	60	195

Following the same procedure as in Appendix III and IV, the following results were obtained.

Source	Sum of Squares	Degrees of Freedom	Variance estimate
Between	158700.54	2	79350.27
Within	368139.38	45	8180.87
Total		47	F = 9.69

Following a significant overall F the Newman Keuls' test was applied. (Steel and Torrie, 1960. Page 110). Results are given in Table 2, page 24.

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